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MALE REPRODUCTIVE STRATEGIES IN WILD NORTHERN PIG-TAILED MACAQUES (MACACA LEONINA): TESTING THE PRIORITY-OF-ACCESS MODEL

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by

Florian Trébouet

M.S., Bordeaux Sciences Agro, 2011

A Dissertation
Submitted in Partial Fulfillment of the Requirements for the
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DISSERTATION APPROVAL

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AN ABSTRACT OF THE DISSERTATION OF

Florian Trébouet, for the Doctor of Philosophy degree in Anthropology, presented on May 6, 2019, at Southern Illinois University Carbondale.

TITLE: MALE REPRODUCTIVE STRATEGIES IN WILD NORTHERN PIG-TAILED MACAQUES (*MACACA LEONINA*): TESTING THE PRIORITY-OF-ACCESS MODEL

MAJOR PROFESSOR: Dr. Ulrich H. Reichard

Among multi-male, multi-female primate groups, males engage in direct contest competition for access to mates. The priority-of-access model (PoA model) generally predicts that male reproductive success increases with male dominance rank, but the strength of this relationship is expected to decrease with increasing female reproductive synchrony, particularly in seasonally breeding primates. Genetic paternity studies support the model's predictions, having found a positive relationship between male dominance rank and reproductive success. However, in addition to dominance status and female reproductive synchrony, a number of proximate factors also impact males' ability to sire offspring, which have not been considered in studies of male reproductive strategies.

By integrating behavioral, genetic, morphological, and hormonal analysis as more direct measures of reproductive success in individual males, this dissertation investigated the relationship between male dominance rank and reproductive success and including the proximate factors affecting this relationship in wild northern pig-tailed macaques (*Macaca leonina*). The main objectives of this study are: 1) to identify the relationships between male dominance rank, male mating success, and male reproductive success, and assess to what extent female synchrony affects these relationships; 2) to identify the proximate factors that may reduce the reproductive success of the top-ranking male and assess variation in male mating tactics related to dominance rank and migration status (i.e., resident males vs. extra-group males); and 3) to evaluate the function of males' red ornaments that may be used to signal male dominance status (male-male competition) to attract females (female mate choice) or both.

The study was conducted at Khao Yai National Park, northeastern Thailand. Systematic data collection on CH group occurred from September 2015-June 2017. The group composition was recorded daily as well as births, deaths, individual emigrations and immigrations, females' parity status, and the presence of extra-group males (EGMs). Sociosexual data and male-female interactions (i.e., copulations, ejaculatory copulations, consortships, grooming, female proceptive behaviors and receptive behaviors) were recorded during females' receptive periods. To assess male reproductive success, genetic paternity analyses were conducted on fecal DNA samples collected from 18 adult and subadult males, 22 adult females, and 25 juveniles and infants. To measure red skin coloration of males, hindquarter images were collected non-invasively for seven adult males. From those images, skin color and luminance were computationally quantified to assess variation in male anogenital reflectance. Lastly, fecal samples were collected from nine adult males to assess monthly levels of fecal testosterone by microtitreplate enzyme immunoassay.

The distribution of births and matings suggested that northern pig-tailed macaques, at least in this group, are best categorized as moderate seasonal breeders. Indeed, 33-67% of births occurred within a three-month period. Copulation data revealed a positive relationship between male dominance rank and mating success, supporting the predictions of the PoA model. However, the distribution of male reproductive success indicated that: 1) high-ranking males controlled a proportion of paternity much lower than predicted by the PoA model; 2) middle-ranking males controlled a proportion of paternity higher than predicted by the model; and 3) EGMs, not considered in the PoA model, controlled a surprisingly large proportion of paternity despite a low observed mating success. When females were simultaneously receptive, lower-ranking and subadult males engaged in opportunistic and surreptitious copulation and avoided direct competition with higher-ranking males, and most females approached and mated with EGMs out of the resident adult males' sight. However, one EGM also mated in full sight of resident adult males. This is the first study to report mating and successful paternity by EGMs in a moderately seasonally breeding species.

Four male mating tactics were identified: 1) the top-ranking resident male tactic, in which the male competes for the alpha male position to control priority of access to receptive females through long consortships and copulations; 2) the lower-ranking resident male tactic, in which the male copulates opportunistically and surreptitiously out of sight of higher-ranking males mostly during the mating peak; 3) the subordinate EGM tactic, in which the male lives semi-solitarily and copulates opportunistically and surreptitiously, mostly during the mating peaks; and 4) the super-dominant EGM tactic, in which the EGM copulates irrespective of the presence of other males and in full sight of even the highest-ranking resident male.

In addition, I found support for female mate choice. Darker and redder males had more mating partners, received more female proceptive behaviors, and were engaged in more consortships and grooming with receptive females. Furthermore, males became redder and darker as female reproductive synchrony increased. Together, these results suggest that male red ornaments exhibited in the male's anogenital area is attractive to females. Furthermore, behavioral evidence of female mate choice towards EGMs was found.

This dissertation provides a comprehensive picture of the complex male mating tactics of northern pig-tailed macaques. To achieve reproductive success, males engage in a diversity of mating tactics, strongly influenced by male dominance rank and the degree of female

reproductive synchrony. However, mate-guarding costs, surreptitious copulations by lower-ranking males and EGMs, and female mate choice, need to be included in an extended version of the PoA model to provide stronger predictions of the distribution of male reproductive success in primates.

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DEDICATION

Pour mes parents
To my parents

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CHAPTER 1

INTRODUCTION

1.A. Brief Theoretical Framework

Like all organisms, primates are subject to the evolutionary process described by Darwin as evolution by natural selection (Darwin, 1859). Individuals must survive and reproduce. Resources in the environment are limited, forcing individuals to compete to achieve the ultimate goals of reproduction and survival (Darwin, 1859). However, within the struggle of survival and reproduction, there are different ways in which to achieve this goal. With regard specifically to achieving reproduction, individuals follow different strategies, the success of which is measured as their reproductive output (Darwin, 1859). Primate males are known to use a variety of reproductive strategies; those living in multi-male, multi-female groups are often characterized by strong male-male competition over access to females and females are often considered being choosy regarding their partner choice (Clutton-Brock, 2004). Comparative studies suggest a positive correlation between male dominance rank and reproductive success among primate species, with a reproductive advantage for the top-ranking male, commonly designated the alpha male (Cowlishaw & Dunbar, 1991; Majolo, Lehmann, de Bortoli Vizioli, & Schino, 2012; Surbeck, Langergraber, Fruth, Vigilant, & Hohmann, 2017; van Noordwijk & van Schaik, 2004).

However, the strength of the relationships between dominance rank and male reproductive success has been shown to vary substantially across primates and can even be weak or absent (e.g., Kutsukake & Nunn, 2006; van Noordwijk & van Schaik, 2004).

One main factor that is believed to affect the relationship between male dominance rank and reproductive success is the degree of female reproductive synchrony (female synchrony), i.e., the number of simultaneously sexually receptive females in one group (Paul, 2002; Setchell, 2008; van Noordwijk & van Schaik, 2004; van Schaik, Pradhan, & van Noordwijk, 2004). As the number of simultaneously receptive females increases, the alpha male has more difficulty in monopolizing all receptive females, which may allow females to copulate with another male of their choice such as a lower-ranking male (Cowlishaw & Dunbar, 1991). Based on a study in rhesus macaques (*Macaca mulatta*), Altmann (1962) developed a model, which predicts the effect of female synchrony on the relationship between dominance rank and male reproductive success. The model assumes that the highest-ranking males in a group will have priority of access to copulate with and to fertilize receptive females, which has become known as the Priority-of-Access or PoA model. The model also considered that as female reproductive synchrony increases, the ability of the highest-ranking male to control access to multiple sexually active females will decrease, allowing also lower-ranking males to sire offspring.

Studies that have tested the PoA model generally supported the model’s predictions, verifying a positive correlation between predicted and observed mating/reproductive success (Alberts, Buchan, & Altmann, 2006; Boesch, Kohou, Néné, & Vigilant, 2006; Dubuc, Muniz, Heistermann, Engelhardt, & Widdig, 2011; Engelhardt, Heistermann, Hodges, Nürnberg, & Niemitz, 2006; Setchell, Charpentier, & Wickings, 2005a; Sukmak, Wajjwalku, Ostner, & Schülke, 2014). However, in those studies, the model overestimated the ability of the top-ranking male to monopolize copulations and paternity in the group, while it underestimated the ability of the lower-ranking males to copulate with females and sire offspring. The discrepancy between the predicted and actual reproductive success of top-ranking male was even more pronounced in species with relatively high female synchrony, especially in seasonally breeding species (Dubuc et al., 2011). In addition to female synchrony, several proximate factors have been proposed to explain the residual variation from the mating/reproductive success predicted by the PoA model: energetic constraints of mate-guarding on males, surreptitious copulations, stability of the dominance hierarchy, male sexual coercion, the number of male competitors, presence of extra-group males, and female mate choice (Alberts, 2012; Alberts, Watts, & Altmann, 2003; Bissonnette, Bischofberger, & van Schaik, 2011; Port & Kappeler, 2010; Young, Hähndel, Majolo, Schülke, & Ostner, 2013).

1.B. Objectives of the Dissertation

To date, studies of the PoA model and proximate factors affecting the relationships between male dominance rank and reproductive success remain scarce, especially in moderately and strictly seasonally breeding primates (reviewed by Dubuc et al., 2011). Further, most of those studies have been using an indirect measure of reproductive success (i.e., mating success, instead of genetic paternity analyses). By integrating behavioral, genetic, morphological, and hormonal analysis as more direct measures of reproductive success in individual males, this dissertation seeks to answer the question: What is the relationship between male dominance rank and reproductive success and what are the proximate factors affecting this relationship in wild northern pig-tailed macaques (*M. leonina*)?

The northern pig-tailed macaque is an appropriate model to investigate this question because: 1) they live in a multi-male, multi-female social system with a clear dominance hierarchy and marked sexual dimorphism in body size, signaling direct male contest competition for access to females; 2) their degree of reproductive seasonality remains unclear, but females have been reported to be simultaneously receptive, which may affect the ability of the alpha male to monopolize access to females; 3) both males and females may have multiple mating partners, and females may be able to choose their mating partner; and 4) males exhibit a red coloration in the anogenital area, which has been suggested to be used as a signal of dominance status, to attract females, or both (Carlson, 2011; Choudhury, 2008; Feeroz, 2003). Altogether, these characteristics suggest that several proximate factors may affect the alpha male's ability to control access to females in this species. Furthermore, little is known about the reproductive strategies of wild northern pig-tailed macaques as most studies on this species have been conducted on captive groups (Carlson, 2011; Choudhury, 2008; Feeroz, 2003).

While the specific hypotheses and predictions guiding my dissertation research will be presented with the corresponding chapters that present my data analyses and results (see Chapters 4-6), the general main objectives of my dissertation can be summarized as follows:

1) My first objective is to identify the relationships between male dominance rank, male mating success, and male reproductive success, and assess to what extent female synchrony affects these relationships (see Chapter 4). For this objective, I will test the accuracy of the PoA model's predictions.

2) My second objective is to identify the proximate factors that may reduce the reproductive success of the top-ranking male and assess variation in male mating tactics related to dominance rank and migration status (i.e., resident males vs. extra-group males) (see Chapter 5).

3) My third objective is to evaluate the function of males' red ornaments which may be used to signal male dominance status (male-male competition), to attract females (female mate choice), both. For this objective, I will investigate the relationships between male sexual skin coloration, dominance rank, sociosexual behavior, and testosterone (see Chapter 6).

In addition, in Chapter 2, I will present a synthetic background of the macaque species, including the study species (i.e., their ecology, evolution, distribution, social organization, and mating strategies), and a general overview of the methods used in this dissertation research. In Chapter 3, I will describe the demography, social organization, male dominance relationships, and reproductive seasonality of the study group. Because of the rarity of study on wild northern pig-tailed macaques, the question about the species' reproductive seasonality remains inconclusive (Carlson, 2011; Choudhury, 2008; Feeroz, 2003) and data regarding demography, social organization, and dominance relationships are sorely needed. The results of Chapter 3 will be used as background data for the following chapters focusing on male mating tactics (Chapter 4-6). Finally, in Chapter 7, I will combine and discuss the results of the previous chapters, and then expand on the greater contributions of my findings to macaque reproductive strategies.

1.C. Literature Review

The following section provides the general, broad framework of ideas, theories, and significant literature that contextualizes my dissertation and that is necessary to understand my dissertation research. To keep this introduction comprehensive, more detailed and specific literature reviews targeting particular topics that I investigated and that were used to develop testable hypotheses and predictions will follow in the corresponding chapters that also present my data analyses and results (Chapters 3-6).

1.C.1. Sexual selection theory

Within the framework of the theory of evolution by natural selection (Darwin, 1859), Charles Darwin developed the theory of sexual selection which he mainly discussed in his classic book, *The Descent of Man, and Selection in Relation to Sex* (1871). From his observations on the train of peacock, the coloration of bird-of-paradise, and the sexual swelling of female chimpanzee, Darwin realized that these sexually dimorphic traits, which are sex differences related to reproductive functions (Darwin, 1871), did not confer advantage over survival or direct production of offspring, but over competition for access to mating opportunities. Darwin defined "sexual selection" as selection that "depends on the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction" (1871:209). Individuals competing for mates among same-sex individuals may evolve traits that would improve their chance of acquiring mates (Darwin, 1871). In other words, sexual selection is "a form of natural selection that acts differently on the two sexes" (Kappeler & van Schaik, 2004:4) and is "due to variance in reproductive success among members of the same sex and species" (Gowaty, 2004:37). Sexual selection is therefore a special category of natural selection that favors traits that increase reproductive success through mate competition and mate choice with usually a stronger selection for traits in the sex that is limited by the number of mates from the opposite sex (Manson, 2011).

Within sexual selection, Darwin recognized two fundamental driving forces: intrasexual selection, which results from mate competition, and intersexual selection, which results from mate choice (Clutton-Brock, 2004). Intrasexual selection is defined as selection among same-sex individuals related to competition for mating partners, whereas intersexual selection is defined as selection between opposite sexes as a consequence of mate choice (Clutton-Brock, 2004). From his observations, Darwin mainly described these two driving forces as male-male competition for access to females and female mate choice of the most attractive males (Clutton-Brock, 2004). Variation of sexually selected male traits, such as weapons or ornaments, give an advantage to males to fight other males or attract females, which compensate for the costs of developing these traits in terms of resource investments and potentially greater predation risk (Manson, 2011). Darwin (1871) identified weapons and ornaments as secondary sexual characteristics that are used in intrasexual and intersexual competition for mates to reproduce, respectively. He differentiated these characteristics from primary sexual characteristics that are directly related to the act of reproduction. The concepts of male-male competition and female mate choice have helped advance our understanding of (mainly) male secondary sexual characteristics, which can increase a male’s fitness compared to competing males (Gowaty, 2004). However, even though intrasexual selection was recognized by biologists, the selection of exaggerated male traits by female mate choice was neglected and did not play a prominent role in theoretical and empirical sexual selection studies until the mid-Twentieth Century (Huxley, 1938; Manson, 2011).

1.C.2. Sex roles and intersexual conflict

Classical laboratory studies in the mid-Twentieth Century by Bateman (1948) reinforced Darwin's views and produced empirical support for the idea that females invest more in producing gametes than males. Females greater initial reproductive investment was interpreted to mean that females would be ‘choosy’ as they stand to risk more in mate choice (lose more from choosing a poor mate), and therefore they would more strongly discriminate amongst competing males and only chose a partner of high quality. In contrast, males (who produce “cheaper” gametes) would have little to lose from risky mating or possible poor mate choice with regard to a female’s reproductive potential, and therefore would sexually behave rather indiscriminately regarding female partners. Bateman (1948) argued forcefully that females were primarily constrained by access to resources and males by access to reproductively active females. Williams (1966) and Parker and colleagues (1972) also argued that females needed more energy to produce one egg than males would need to produce one sperm (or even a sperm packet) due to the enormous size difference between egg and sperm. The difference between male and female reproductive strategies was thus explained by the type of gametes that they produced. This view was extended by Trivers (1972), who considered sex differences not to end at gamete production but to be a function of overall relative parental investment, rather than gamete size alone (Kappeler & van Schaik, 2004). Trivers (1972:139) defined parental investment as "[…] any investment [in time, energy, or risk] by the parent in an individual offspring that increases the offspring's chance of surviving [...] at the cost of the parent's ability to invest in other offspring". According to this view, the sex that invests more in parental care, in general the female, is the limiting resource for the opposite sex, the male (Trivers, 1972).

Evidence against the idea of ubiquitously choosy females was brought forward by Hrdy in 1977 for species with female-biased parental investment, such as the primates, following her long-term field research on free-ranging Hanuman langurs, *Presbytis entellus* (Gowaty, 2004). Hrdy (1977) was the first scientist to emphasize the role of infanticide as an evolved male reproductive strategy, which she argues spurred the evolution of female promiscuity as a counter-strategy and thus the deviation from generally assumed female coyness. She argued that a male, who took the top-ranking position in the group, may benefit from killing nursing infants that were not fathered by him, causing the female to resume cycling and become sexually receptive sooner than if she had completed nursing the infant. Then, the top-ranking male would have a greater probability of being the father of the female's next infant, which would potentially increase his reproductive success beyond what he could have achieved had he "waited" for the female to complete lactation. Although this strategy enhances males' reproductive success, it severely and negatively affects females' reproductive success (Hrdy, 1977).

Hrdy (1977) hypothesized that females evolved a counter-strategy to male infanticide by increasing promiscuity in order to confuse paternity among males. Indeed, males were assumed to be unable to detect the true timing of ovulation and would be left with using copulation as a proxy for determining if they had sired an infant with the female. Consequently, by mating polyandrously with many males, females in their fertile period would reduce paternity probability of a dominant male while increasing paternity probability for other males, which would guard against the probability of male infanticide in case a male-change would occur at the time the female would be lactating an infant. Further, by mating outside the fertile period, females would influence males' assessment of paternity chances (Hrdy, 1979; van Schaik et al., 2004). Thus, a male with a small but non-zero probability of paternity is unlikely to commit infanticide if even a small risk of killing his own offspring exists (Hrdy, 1979). Hrdy's results helped to open a discussion beyond the "choosy females" concept by highlighting the adaptive value of promiscuity for female reproductive success, and her work stimulated future study in this direction (Gowaty, 2004).

It was only in the late Twentieth Century that a new form of sexual selection was hypothesized, called intersexual conflict (Parker, 1979), which became explicitly recognized as the third driving force of sexual selection (van Schaik et al., 2004). Parker (1979) emphasized that the reproductive strategies of males and females are in conflict due to the divergent evolutionary interests of males and females. Sexual coercion varies between species and is thought to be related to mating system and male-male competition (Kappeler, 1999). The male strategies are particularly costly to females, who are then expected to evolve counter-strategies (van Schaik et al., 2004). Hrdy's observation of infanticide in Hanuman langurs is an example of sexual coercion and the emergence of intersexual conflict (Hrdy, 1977; van Schaik et al., 2004). As male infanticide is detrimental to female reproductive success, female promiscuity and paternity confusion become a beneficial strategy to the extent that it decreases the probability of male infanticide (Zinner, Nunn, van Schaik, & Kappeler, 2004).

In addition, in various genera and species of Old World monkeys and apes, females develop a signal that conceals the time of ovulation. As a result, females may copulate with several mates and thus the paternity probability is shared among several males, which decreases the risk of infanticide (Hrdy, 1977). On the other hand, females may find a benefit by concentrating copulations with a top-ranking male that will ensure protection of their offspring out of his own reproductive interests (Palombit, Seyfarth, & Cheney, 1997). Furthermore, high male dominance rank may be associated with a greater ability to compete and gain access to resources. Thereby, male offspring of a female who conceived with a high-ranking male may indirectly benefit from her sons’ inheriting "good quality" genes, assuming that competitive ability is heritable (Pagel, 1994). In such cases, females would in fact benefit from signaling the time of ovulation to attract a high-ranking male (Nunn, 1999b). In this model, called the female dilemma, females are divided between confusing paternity to counter potential male infanticide and biasing paternity towards a favored male who could offer effective protection to an infant and superior genetic qualities (Nunn, 1999b). Other examples of intersexual conflict are male sexual harassment, forced copulation, and prolonged mate-guarding, which maximize the male's reproductive success, but may decrease a female’s fitness (Clutton-Brock & Parker, 1995; Hrdy, 1974; Smuts & Smuts, 1993; Zinner et al., 2004).

Since the 1970s, sexual selection theory including competition over access to mates, mate choice, and intersexual conflict has experienced a renewed interest by the scientific community, which has brought new theoretical insights and empirical evidence to the field (Paul, 2002). Studies have shown that neither mate competition, nor mate choice, can be restricted to one sex and that these expressions can take different forms (Cunningham & Birkhead, 1998; Johnstone, Reynolds, & Deutsch, 1996). For example, male-male competition is not always reflected in males fighting, but may also be characterized by scramble competition where males compete to locate and mate with females before rivals can do so (Paul, 2002). Wiley and Poston (1996) have clarified Darwin's mechanisms of sexual selection. On the one hand, mate competition is defined as a set of behaviors that increase an individual’s number of potential mates (Wiley & Poston, 1996). On the other hand, mate choice subsumes all behaviors displayed by individuals of one sex that lead them to be more likely to copulate with certain individuals of the opposite sex than others (Halliday, 1983) and thus decreasing, instead of increasing, the set of potential mates (Paul, 2002; Wiley & Poston, 1996).

1.C.3. Male reproductive strategies in primates

Traditionally, in multi-male, multi-female group-living primates, the primary male reproductive strategy is to monopolize receptive females, the limiting resource to male reproductive success (Trivers, 1972). Typically, males are ordered into a dominance hierarchy through direct contest competition (i.e., fighting ability), which will determine their access to receptive females (Altmann, 1962; Emlen & Oring, 1977; Fedigan, 1983). According to the Priority-of-Access model (PoA model), male reproductive success is based on the male's dominance rank and female synchrony (the number of simultaneously receptive females) (Altmann, 1962). The model predicts that the top-ranking males will have priority of access to fertilize receptive females. Therefore, a positive relationship between male dominance rank and reproductive success is predicted. However, as female synchrony increases, the highest-ranking males' ability to control access to receptive females is reduced, allowing lower-ranking males to also fertilize receptive females. Therefore, as female synchrony increases, the strength of the relationship between male dominance rank and reproductive success is predicted to weaken.

So far, the PoA model has been only thoroughly tested with paternity analyses in a few species (e.g., savanna baboons, *Papio cynocephalus*, Alberts et al., 2006; Engelhardt et al., 2006; mandrills, *Mandrillus sphinx,* Setchell et al., 2005a; chimpanzees, *P. troglodytes,* Boesch et al., 2006; rhesus macaques, Dubuc et al., 2011; further details see Chapter 4), finding a predicted positive relationship between male dominance rank and reproductive success. More recently, however, it has been recognized that male-male competition, and thereby the expectations of the PoA model, can be influenced by additional factors, such as energetic constraints of mate-guarding on males, surreptitious copulations, stability of dominance hierarchy, male sexual coercion, the number of male competitors, presence and number of extra-group males, and female mate choice (Alberts, 2012; Alberts et al., 2003; Bissonnette et al., 2011; Port & Kappeler, 2010; Young, Hähndel, et al., 2013).

To overcome the primary reproductive tactic of using male-male dominance to monopolize receptive females, males may develop alternative reproductive tactics (ARTs) (Setchell, 2008;

Young, Hähndel, et al., 2013). Before further elaborating on the ARTs, I want to make a distinction between the terms “tactic” and “strategy,” as the boundary between the meaning of those two terms is often ambiguous in studies of ARTs (Taborsky, Oliveira, & Brockmann, 2008). “Tactic” and “strategy” are associated to the same particular function (e.g., attracting mates), but at different levels—“tactics” refer to phenotypic traits whereas “strategies” reference genotypic traits (Brockmann, 2001; Taborsky et al., 2008). Indeed, ARTs refer to “the presence of two or more discrete behavioral variants among adults of one sex and one population when those variants serve the same functional end” (Brockmann, 2001:6). Thus, while “alternative reproductive strategies” are related to genetic differences, “alternative reproductive tactics” are related to decision-making processes of an individual (Brockmann, 2001). In this dissertation, I will therefore often prefer to use the term “tactic” because I am mainly focusing on behavioral traits.

ARTs of males vary among primates (Setchell, 2008). For instance, lower-ranking males and extra-group males (EGMs) may engage in opportunistic and/or surreptitious copulations, which are common in many primate species and have been confirmed to result in fertilizations (reviewed by Setchell, 2008; for further details, see Chapter 5). Male sexual coercion is another form of ARTs (Smuts & Smuts, 1993). Indeed, due to marked sexual dimorphism in body weight and strength, males may force copulation with a female refusing to copulate, which maximizes the male's reproductive success but may decrease the female's fitness as it may go against the female mate preference for other males (Smuts & Smuts, 1993). Over their lifetime, individuals may engage in variable ARTs in response to other members of the group, the environment, and also age, size, sex, and other abilities of an individual (Andersson, 1994).

Furthermore, males may also compete at the post-copulatory level through sperm competition (Dixson, 2012). This form of competition occurs when females copulate promiscuously during their fertile period. Factors such as sperm number, vitality and/or viability have been recognized to potentially affect the chance of siring offspring in primates (Eberhardt, 1996; Reeder, 2003). Thus, the males who can produce sperm in higher quantity and/or quality, and can copulate the most with fertile females, will have a higher chance of siring offspring (Eberhardt, 1996; Reeder, 2003). However, postcopulatory mechanisms in primates remain poorly understood, mainly due to difficulties of conducting experimental studies (Setchell, 2016).

Lastly, as primates are characterized by remarkably slow life histories, low reproductive rates, and high maternal investment (Jones, 2011), it has been hypothesized that female selectivity should be strong in mate choice and therefore affect male reproductive strategies (Andersson, 1994; Trivers, 1972). Recent studies, based on genetic paternity analyses, have found evidence on the diversity and efficacy of female mate choice in primates (reviewed by Manson, 2011). Indeed, females may prefer to copulate with high-ranking males, which may signal "good genes" that will increase the fitness of the females’ offspring (Mays & Hill, 2004) or greater access to reproductively valuable resources and better protection by those high-ranking males (Manson, 2011). Females may also prefer to copulate with males that exhibit redder skin colors (e.g., Dubuc, Allen, Maestripieri, & Higham, 2014; Setchell, 2005), which may be used as an honest signal of genetic quality (e.g., Setchell, 2016; for further details, see Chapter 6). Furthermore, females may prefer to copulate with unrelated/unfamiliar males to avoid inbreeding or to increase the heterozygosity of the offspring (Manson, 2011).

In multi-male, multi-female group-living primates, the top-ranking male generally controls access to receptive females, but his ability to monopolize females is affected by proximate factors, such as reproductive seasonality and female mate choice that can lead to male ARTs. Reproductive seasonality of a species is an important factor to consider because, as female reproductive synchrony increases, the reproductive skew towards the top-ranking alpha male is predicted to decrease (Altmann, 1962; Kutsukake & Nunn, 2006). However, studies that investigated the effect of female synchrony on male dominance rank and reproductive success using a direct measure of reproductive success, through genetic paternity testing, have remained limited so far, especially in moderately and strictly seasonally breeding species (e.g., Japanese macaques, *M. fuscata*, Hayakawa, 2007; Barbary macaques, *M. sylvanus*, Bissonnette et al., 2011; rhesus macaques, Dubuc et al., 2011). In these species in which the degree of female synchrony is high, effects of proximate factors are expected to be even more pronounced, and consequently, males are expected to be more likely engaged in ARTs (Dubuc et al., 2011). Because of a lack of empirical studies, further investigations that identify the proximate factors leading to the development of male ARTs in relation to the degree of female synchrony are thus needed.

To comprehensively recognize primate reproductive strategies, it is also important to understand the evolutionary origin and function of skin coloration in relation to the mating system. Indeed, colorful ornaments affect relationships between and within the sexes through female mate choice and male-male competition (Petersdorf, Dubuc, Georgiev, Winters, & Higham, 2017). However, the adaptive function of ornaments has been meticulously studied in only a handful of species (e.g., mandrills, Setchell, 2016; drills, *M. leucophaeus*, Marty, Higham, Gadsby, & Ross, 2009; rhesus macaques, Petersdorf et al., 2017), and further inquiry on this topic is needed to fully grasp male reproductive strategies in primates.

CHAPTER 2

MATERIAL AND METHODS

In this chapter, I will present a synthetic background on macaque distribution, evolution, ecology, social organization, and mating strategies, which will be followed by a similar overview of the northern pig-tailed macaques (*Macaca leonina*), the study species. Then, I will provide a general overview of the site and study group as well as the methods used in this research in order to guide the reader about the directions of this dissertation. More detailed information of study methods (data collection and analysis) used to test the corresponding hypotheses and predictions will be given in the following chapters (Chapters 4-6).

2.A. Overview of the Macaque Genus

The name “macaque” has been suggested to originate from the Portuguese word *macaco*, which originally derived from the western African language Fiot word *makaku*, meaning monkey (Roos & Zinner, 2015). The genus *Macaca* represents one of the most successful primate radiations with one of the widest geographical distributions of any non-human primates (Fooden, 1982). The 23 species are distributed throughout southern and eastern Asia, reaching as far as China and Japan, and relic populations of macaques are still found in Northern Africa (Fooden, 1982). According to Thierry (2007:224), macaque societies are best characterized by “both a profound unity and a great diversity”. Indeed, macaques share the same basic patterns of social organization (e.g., multi-male, multi-female groups) but they also show great variation of behaviors (e.g., affiliative, aggressive, and sexual) (Thierry, Singh, & Kaumanns, 2004). In this section, I review the evolution, ecology, social organization, and mating systems of macaques to unravel their unity and diversity.

2.A.1. Macaque morphology, taxonomy, and evolution

Macaques are part of the genus *Macaca*, a major lineage of the family Cercopithecidae (Old World monkeys). Together with baboons (genus *Papio*), geladas (*Theropithecus*), mandrills (*Mandrillus*), mangabeys (*Cercocebus* and *Lophocebus*), and kipunjis (*Rungwencebus*), they form the tribe Papionini within the subfamily Cercopithecinae, which includes more than 40 species (Jaffe & Isbell, 2011; Swedell, 2011; Thierry, 2011).

Macaques are medium-sized primates (adult weight 2-30 kg) and share great similarities in dental, cranial, and postcranial anatomy with other members of the subfamily Cercopithecinae, including cheek pouches, long faces, high crowned-molar teeth, and 42 chromosomes (Delson, 1980; Thierry, 2011). However, macaque’s limbs are generally more slender than those of baboons, geladas, mandrills, and mangabeys, but more robust than those of guenons (Fleagle, 2013). Macaques are also characterized by variable expression of sexual dimorphism in body mass (adult females’ weight, 3-11 kg; adult males’ weight, 5-18 kg; Smith & Jungers, 1997) and canine size (ratio of adult male/adult female mean upper projective canine height: 1.93-2.61; Plavcan & van Schaik, 1992) but to a lesser degree than baboons and mandrills.

Macaques originated in Africa about 9-10 Ma when they split from the rest of the Papionini (Fleagle, 2013; Raaum, Sterner, Noviello, Stewart, & Disotell, 2005). The macaque ancestors entered Europe from North Africa around 5.5 Ma, probably via the Levant (Delson, 1980; Thierry, 2011), and subsequently, spread to eastern and southern Asia (Fleagle, 2013; Fleagle & McGraw, 1999). In less than 3 million years, macaques radiated into different species groups (Fleagle, 2013; Tosi, Morales, & Melnick, 2003), which match the different phyletic groups of macaques found today in North Africa and Asia (see below). Presently, most taxonomists recognize 23 species in the genus *Macaca* based on genital morphology, geographical distribution, and behavioral and genetic data (Fan et al., 2017; Roos & Zinner, 2015; Thierry, 2011; Zinner, Fickenscher, & Roos, 2013). While some of those species are geographically isolated, most of them have broad areas of overlap in their distributions (Thierry, 2011).

Macaques have been divided into species groups, although the exact number of species in each group has been much debated since the 1970s (Delson, 1980; Fooden, 1976, 1980; Groves, 2001). According to the most recent classification (Zinner et al., 2013), macaques can be divided into seven species groups because this best reflects their evolutionary history (Roos et al., 2014; Roos & Zinner, 2015; Zinner et al., 2013). Three species groups are monotypic (i.e., only one species is found in each group) and four are polytypic groups with several species. Species groups have been composed by Zinner and colleagues (2013) as follows:

1) Sylvanus group, including Barbary macaques (*M. sylvanus*).

2) Silenus group, including lion-tailed macaques, (*M. silenus*), northern pig-tailed macaques (*M. leonina*), southern pig-tailed macaques (*M. nemestrina*), Siberut macaques (*M. siberu*), and Pagai Island macaques (*M. pagensis*).

3) Sulawesi macaques group, including Celebes crested macaques (*M. nigra*), Gorontalo Macaques (*M. nigrescens*), Heck’s macaques (*M. hecki*), Tonkean macaques (*M. tonkeana*), Moor macaques (*M. maura*), and booted macaques (*M. ochreata*).

4) Sinica group, including toque macaques (*M. sinica*), bonnet macaques (*M. radiata*), Arunachal macaques (*M. munzala*), Tibetan macaques (*M. thibetana*), Assamese macaques (*M. assamensis*), and white-cheeked macaques (*M. leucogenys*).

5) Arctoides group, including stump-tailed macaques (*M. arctoides*).

6) Fascicularis group, including long-tailed macaques (*M. fascicularis*).

7) Mulatta group, including rhesus macaques (*M. mulatta*), Formosan macaques (*M. cyclopis*), and Japanese macaques (*M. fuscata*).

The monotypic Sylvanus group is the most ancestral macaque group based on genetic data (Li et al., 2009) and originated in Africa and is found today in northwestern Africa and Gibraltar (Delson, 1980; Groves, 2001; Thierry, 2011; Zinner et al., 2013). The Silenus group diverged from the Sulawesi macaques group around 3 Ma (Liedigk, Roos, Brameier, & Zinner, 2014; Perelman et al., 2011; Tosi et al., 2003; Ziegler et al., 2007) and the geographical distribution of the five species of this group ranges from eastern India and southern China to Indonesian islands (Roos & Zinner, 2015). The Sulawesi macaque group originated in the island of Sulawesi (Indonesia) around 2-3 Ma and diverged rapidly into six parapatric species (i.e., ranges of these species are adjacent to each other) (Zinner et al., 2013). However, their speciation was allopatric (i.e., non-overlapping geographical area). Indeed, during the Pleistocene, Sulawesi was an archipelago of several different islands isolated from each other which led to the rapid diversification of Sulawesi macaques (Thierry, 2011). Because of this relatively fast speciation, the phylogenetic relationships among these species are still not well understood (Roos & Zinner, 2015).

The Sinica group started to diverge around 3.5 Ma (Liedigk et al., 2014; Perelman et al., 2011; Tosi et al., 2003) and the five species of this group are widely distributed from Nepal, China to southern India, Sri Lanka and northern Vietnam (Roos & Zinner, 2015). Further research is needed to understand the phylogenetic relationships within the group species (reviewed by Roos & Zinner, 2015). The monotypic Arctoides group evolved 2-3 Ma and likely resulted from an hybridization between the ancestors of the Sinica group and the Mulatta group (Roos & Zinner, 2015; Thierry, 2011). *M. arctoides* is now widely distributed in Southeast Asia (Roos & Zinner, 2015; Thierry, 2011).

The Mulatta group is one of the most recent radiations of macaques (Thierry, 2011), and the three species of this group have an extended distribution including Japan, Taiwan, and most of the continental part of Asia and Southeast Asia (Fooden, 1980). In this group, rhesus macaques have the widest distribution of all macaques, ranging from eastern China to Afghanistan (Fooden, 1980). Lastly, the Fascicularis group includes only the long-tailed macaques and ranges over a large area including the southern part of the southeast Asian mainland, most of the Sudaland (Borneo and Sumatra), and Philippines (Fooden, 1995).

It has been argued that the Pleistocene played a major role in the evolution of macaques (Brandon-Jones, 1996; Eudey, 1980). During this epoch, periods of glaciation and deglaciation affected the habitat of macaques, creating from time to time geographical barrier because of large river formation, deforestation, and increase of sea level (Thierry, 2011). These events isolated different population but also allowed the dispersal of other populations. Thus, it is likely that historical contingencies have largely contributed to the great radiation and wide distribution of macaques (Thierry, 2011).

2.A.2. Macaque habitat and ecology

Macaques are semiterrestrial primates that inhabit a wide variety of habitats and climates, from lowland to high altitude, from tropical climate to regions with snow in winter, and from evergreen forest to grasslands or semideserts (Fooden, 1982; Richard, Goldstein, & Dewar, 1989). While some species (e.g., long-tailed macaques and rhesus macaques) live in diverse types of habitat, other species have a limited ecological range (e.g., lion-tailed macaques and southern pig-tailed macaques limited to primary broadleaf evergreen forest) (Thierry, 2011). Several macaque species (e.g., long-tailed macaques, rhesus macaques, toque macaques, and bonnet macaques) even have the ability to live in close proximity to humans and successfully exploit human-modified environments (Richard et al., 1989), which often lead to conflicts on farm lands, at tourist sites, and in urban contexts (Priston & McLennan, 2013). However, in Asian countries, macaques are often tolerated, respected, and have been integrated in religious mythology and local cultures.

Although macaques are considered to be mainly frugivorous, most species have highly flexible diets that include diverse plant parts (e.g., seeds, leaves, flowers, roots), invertebrates, and small vertebrates (Ménard, 2004; Thierry, 2011). During periods of fruit shortage, tropical species such as southern pig-tailed macaques, long-tailed macaques, and Formosan macaques switch to a diet including mainly leaves or invertebrates (Thierry, 2011). In temperate regions, fruit production may be more limited and macaques must rely on other food sources (Thierry, 2011). In Japan, Japanese macaque groups in cool-temperate regions (e.g., Kinkazan) are more granivorous than the ones in warm-temperate regions (e.g., Yakushima), which are more frugivorous (Ménard, 2004). Barbary macaques from Northern Africa are mainly either granivorous or folivorous, while the widely distributed rhesus macaques are mainly folivorous but they can also be frugivorous on occasions or rely heavily on agricultural crops or food from people (Richard et al., 1989). Thus, macaques overall occupy diverse ecological niches with remarkable ecological plasticity.

2.A.3. Macaque social organization, mating systems and relationships

2.A.3.a. Social organization. All macaque species share the same basic social organization type characterized by a multi-male, multi-female group with overlapping home ranges of neighboring groups (Thierry et al., 2004). However, there are some exceptions of individual populations that live in a single-male, multi-female group (Thierry et al., 2004). Macaque groups contain both adult males and females with offspring, ranging typically from 10-100 individuals (Thierry, 2011). The adult sex ratio is female-biased, but the ratio varies from elevated female bias in southern pig-tailed macaques and lion-tailed macaques to an almost balanced sex ratio in Barbary macaques (Thierry, 2011). While females are phylopatric (i.e., remain in their natal group) and form kin-bonded subgroups (matrilines) within their natal group, males disperse to adjacent groups before sexual maturity and usually migrate several times during their life between social groups (Gachot-Neveu & Ménard, 2004; Melnick & Hoelzer, 1992; Thierry et al., 2004).

Comparative studies of agonistic interactions have led to the classification of macaques into four social styles (Grades 1-4) based on patterns of aggression and reconciliation (Thierry, 2008, 2011). At one end of the spectrum, species from grade 1 (rhesus macaques, long-tailed macaques) are characterized by unidirectional, high-intensity conflicts, and low levels of reconciliation (dominance asymmetry). At the other end of the spectrum are species forming grade 4 (e.g., Tonkean macaques, Celebes crested macaques), which are characterized by bidirectional, low-intensity conflicts, high levels of affiliative behaviors, and behaviors that reduce social tension. Species of grades 2 (e.g., long-tailed macaques, southern pig-tailed macaques) and 3 (e.g., lion-tailed macaques, stump-tailed macaques), are intermediate between the two previous grades. These social styles represent covariant sets of social characters which stem from the different social relationships and individual characters found in macaques (Thierry, 2011).

It is important to note that the social style of a species cannot predict the level of intermale competitive reproductive strategies in a group because both mechanisms are disconnected (Soltis, 2004; Thierry, 2011). Indeed, the social relationships of a species cannot predict the outcome of intermale competition (Thierry, 2011). Male dominance rank has more effect on male reproductive success in non-seasonally breeding species with limited dominance asymmetry (e.g., Tonkean macaques) than in seasonally breeding species with marked dominance asymmetry (e.g., rhesus macaques) (Thierry, 2011).

2.A.3.b. Mating systems and relationships. Macaques are a very interesting group for studying sexual selection and mating strategies, because they are characterized by a variable level of male reproductive skew and sexual dimorphism and a wide diversity of mating strategies and secondary sexual traits (Dixson, 2012; Soltis, 2004; Thierry, 2011). They have been alternatively described as polygynous (i.e., a single male mating with multiple females) and polygamous (i.e., males and females mating with multiple mates) (Dixson, 2012). Indeed, while male reproductive strategies may be characterized by direct contest competition over access to females (e.g., mate-guarding), surreptitious copulations, endurance rivalry, and sperm competition, female reproductive strategies may include both selective mate choice and mating with several males during or outside a female's conceptive period (Soltis, 2004).

In macaques, interspecific variation of male reproductive skew and male-male mating competition are strongly associated with the species' reproductive seasonality (Brockman & van Schaik, 2005b). In species with year-round copulations (i.e., living in the tropics), male dominance rank is positively correlated with reproductive success and the top-ranking male sires most of the offspring (e.g., long-tailed macaques, de Ruiter, van Hooff, & Scheffrahn, 1994; Engelhardt et al., 2006; stump-tailed macaques, Bauers & Hearn, 1994; crested macaques, Engelhardt, Muniz, Perwitasari-Farajallah, & Widdig, 2017). In seasonally breeding species (i.e., living in temperate regions), the relationships between male dominance rank and reproductive success are weaker and lower-ranking males can be equally or more successful at siring offspring than the top-ranking male (e.g., Barbary macaques, Brauch et al., 2008; Kümmerli & Martin, 2005; Paul, Kuester, Timme, & Arnemann, 1993; rhesus macaques, Berard, Nurnberg, Epplen, & Schmidtke, 1994; Dubuc et al., 2011; Japanese macaques, Soltis, Thomsen, & Takenaka, 2001). Furthermore, in species with year-round copulations, males usually compete over access to females by directly fighting for dominance, whereas in seasonally breeding species, males typically obtain mates through scramble competition and queueing for dominance (i.e., lower-ranking males wait for higher-ranking males to die or emigrate to increase in dominance rank) (van Noordwijk & van Schaik, 2004).

Both males and females have multiple sexual partners. In some species, males are single-mount ejaculators (i.e., male only needs one mount to ejaculate), while in others, males are multiple-mount ejaculators (Soltis, 2004). The significance of this difference of copulation patterns remains to be solved (Soltis, 2004). Males and females often form long-lasting consortships during which they copulate and the male guards the female from other adult males (i.e., mate-guarding) (Soltis, 2004). Depending on the number of simultaneously receptive females, these consortships typically last a few hours but can extend to several days or weeks (Soltis, 2004; Thierry, 2011). High-ranking males engage in longer consortships than lower-ranking males (e.g., rhesus macaques, Manson, 1996; Japanese macaques, Soltis et al., 2001). When lower-ranking males cannot have access to females through direct competition, they may engage in surreptitious copulations out of sight of dominant males.

In addition to direct contest competition, males may compete by endurance rivalries and sperm competition (Soltis, 2004; Thierry, 2011). For instance, male rhesus macaques undergo seasonal fluctuation in body weight that closely correlate with changes in fat storage and the males with the highest weight have the highest reproductive success because fatter males can reduce their feeding time and increase mate-guarding during the mating season (Bercovitch & Nürnberg, 1997). The distribution of paternity can also be affected by sperm competition at the postcopulatory level (Soltis, 2004). Consistent with the fact that sperm competition might favor the production of sperm in macaque species where females mate promiscuously, males in those species have large testes relative to their body size (Dixson, 2012; Harcourt, Harvey, Larson, & Short, 1981; Soltis, 2004). For examples, males with larger testes (relative to body size) enjoyed higher reproductive success than those with smaller testes in rhesus macaques (Bercovitch & Nürnberg, 1996, 1997). Thus, male mating tactics are not solely based on direct competition through fighting, but include also alternative mating tactics that can influence male reproductive success.

In some species, females exhibit sexual skin swelling and reddening in the anogenital and rump area during the periovulatory phase (Dixson, 2012). These cyclical changes of the sexual skin show the greatest fluctuation of shape, color, and size of any primate genus (Dixson, 2012). Pronounced sexual skin swelling is an ancestral trait for macaques, which has been retained in the Sylvanus, Silenus, and Sulawesi macaque groups but has been attenuated or lost to various degrees in the four other groups (reviewed by Bercovitch & Harvey, 2004; Dixson, 2012; Soltis, 2004; Thierry, 2011). Sexual swelling has been the focus of many studies in macaques, with most of them supporting the graded-signal hypothesis (Brauch et al., 2007; Dubuc, Muniz, Heistermann, Widdig, & Engelhardt, 2012; Young, Majolo, Heistermann, Schulke, & Ostner, 2013; reviewed by Soltis, 2004). This hypothesis argues that sexual swellings constitute probabilistic signals that advertise ovulation (Nunn, 1999a). However, studies have also shown that there is variation in the reliability of the sexual swelling signal as an indicator of ovulation among macaques, and that other cues, such as sexual behaviors and olfactory cues, may be more reliable information to males in some species (Higham et al., 2012). Overall, sexual swelling and behaviors vary in their reliability as receptivity signals among macaque species and it is still unclear for many species how sensitive males are to them and how they interpret these signals.

Despite being poorly understood, female mate choice is often observed in macaques (Soltis, 2004). Female macaques may express preference towards particular males by actively soliciting copulations (e.g., rhesus macaques, Dubuc, Allen, et al., 2014; Massen & Sterck, 2013; Overduin-de Vries, Massen, Spruijt, & Sterck, 2012; Japanese macaques, Inoue & Takenaka, 2008; Soltis et al., 2001) or by uttering copulation calls (Maestripieri & Roney, 2005). The characteristics of those favored mating partners by females are diverse. Apart from a preference for high-ranking males (e.g., Barbary macaques, Brauch et al., 2008; Celebes crested macaques, Reed, O'Brien, & Kinnaird, 1997), females appear to also prefer to copulate with low-ranking males (e.g., Japanese macaques, Huffman, 1987, 1992; Soltis, Mitsunaga, Shimizu, Yanagihara, & Nozaki, 1997; Formosan macaques, Birky, 2002), familiar group males (e.g., Japanese macaques Inoue & Takenaka, 2008; Soltis et al., 2001), young adult males (e.g., rhesus macaques, Smith, 1994), or novel/extra-group males (e.g., Japanese macaques Huffman, 1991; rhesus macaques, Bercovitch, 1997; Formosan macaques, Birky, 2002). Furthermore, females have been observed to also prefer to copulate with males exhibiting darker red faces, as found in rhesus macaques (Dubuc, Allen, et al., 2014). The benefits from copulating with those males can be genetic, such as increasing heterozygosity or selection for “good genes”, or non-genetic, such as receiving protection and/or increased access to resources (Manson, 2011). Females also refuse to copulate with particular males, which may be linked to avoiding inbreeding (e.g., Japanese macaques, Soltis, Mitsunaga, Shimizu, Yanagihara, & Nozaki, 1999; rhesus macaques, Manson & Perry, 1993). Despite their selectivity, female macaques often seek to copulate with many males, which increases male-male mating competition and may function to decrease the risks of male infanticide (e.g., Japanese macaques, Soltis et al., 2001; rhesus macaques, Manson, 1992; southern pig-tailed macaques, Oi, 1996; Barbary macaques, Kuester & Paul, 1992; long-tailed macaques, Engelhardt et al., 2006). While cumulative evidence indicates that females actively express mating choices, the (in)direct benefits they receive from their choices, except for the well-documented benefit of inbreeding avoidance, are still largely unclear (Manson, 2011; Soltis, 2004).

Altogether, the mating systems of macaques are complex and remain to be fully understood because they are often species-specific and because of the complex, interactive and sometimes opposing nature of males’ and females’ reproductive strategies (Dixson, 2012; Soltis, 2004;

Thierry, 2011). Most of our knowledge on reproductive strategies of macaques come from a handful of macaque species that have been studied intensively (e.g., long-tailed macaques, Japanese macaques, rhesus macaques, and Barbary macaques). More data of other macaque species are needed to allow comparative studies, which will help to better understand how male and female reproductive strategies and the development of secondary sexual traits are determined by reproductive seasonality, social relationships, and social structure of the group among taxa.

2.B. Distribution, Evolution, Ecology, and Behavior of Wild Northern Pig-tailed Macaques (*Macaca leonina*)

Northern pig-tailed macaques are part of the Silenus group (Fooden, 1976; Groves, 2001; see also 2.A.2. Macaque Morphology, Taxonomy, and Evolution) and are widely distributed from northeastern India, Bangladesh, southern China, and Vietnam to southern Thailand (Fooden, 1976; Groves, 2001; Malaivijitnond et al., 2012). The three species northern pig-tailed macaques, lion-tailed macaques, and Pagai Island macaques were previously considered subspecies of southern pig-tailed macaques, but recent phylogenetic studies recognized them as different species (Delson, 1980; Fooden, 1976, 1980; Malaivijitnond et al., 2012; Rowe, 1996).

The northern and southern pig-tailed macaques (*M. leonina*, *M. nemestrina*, respectively) have been commonly used as models for biomedical research on infectious diseases (e.g., HIV infection and AIDS; Agy et al., 1992; Batten et al., 2006; Beck et al., 2015; Hatziioannou et al., 2009), immunology (Dobard et al., 2012; Shaulov & Murali-Krishna, 2008), neuroscience (Coudé et al., 2011; Rausell, Bickford, Manger, Woods, & Jones, 1998), pathology (Baskin et al., 2004; Hukkanen et al., 2009), and behavior (Bellanca & Crockett, 2002; Sackett, Holm, & Ruppenthal, 1976; Sussman & Ha, 2011). However, our knowledge about pig-tailed macaques in the wild is limited partly because they are shy and difficult to habituate to the presence of observers, and show wide group dispersion and high rates of daily travel (Caldecott, 1986; Choudhury, 2008; Crockett & Wilson, 1980).

Most data on the sociosexual behaviors of northern pig-tailed macaques so far come from only three study populations: one semi-provisioned group at Khao Yai National Park, Thailand (Carlson, 2011), five wild groups at West Bhanugach Forest Reserve, Bangladesh (Feeroz, 2003), and seven wild groups in Assam, North-East India (Choudhury, 2008). The remaining data come from several studies of wild southern pig-tailed macaques (Bernstein, 1967; Bernstein, 1972; Caldecott, 1986; Oi, 1990a; Oi, 1990b; Oi, 1996), and captive studies (e.g., Bullock, Paris, & Goy, 1972; Maestripieri, 1999, 2002, 2005; Nadler & Rosenblum, 1973; Tokuda, Simons, & Jensen, 1968). In captive studies, differentiating northern and southern pig-tailed macaques is usually not possible, because pig-tailed macaques have only recently been split into two species (Malaivijitnond et al., 2012) and most publications before 2012 considered northern and southern pig-tailed macaques one species, *M. nemestrina*, or used the generic term “pig-tailed macaque”.

Northern pig-tailed macaques live in multi-male, multi-female groups, including 13-67 individuals (Carlson, 2011; Choudhury, 2008; Feeroz, 2003). The species is considered semiterrestrial (Albert, Huynen, Savini, & Hambuckers, 2013), although some have considered them mainly arboreal (Choudhury, 2008; Feeroz, 2003). Their habitat is restricted to tropical forests and they are among the most frugivorous of the macaques. Reports vary between 36% of fruit intake in a semi-provisioned group in Thailand (Albert, Huynen, et al., 2013) and 76-87% of fruit intake in a natural food feeding group (Choudhury, 2008; Feeroz, 2003; see Ménard, 2004).

Northern pig-tailed macaques are characterized by considerable sexual dimorphism in body size and weight between males (crown-rump length: 552±3.5 mm, weight: 8.9±0.4 kg, *n*=2, Malaivijitnond et al., 2012; weight: 6.2-9.1 kg, *n*=6, Fooden, 1975) and females (crown-rump length: 456±27.6 mm; weight: 5.1±0.6 kg, *n*=11, Malaivijitnond et al., 2012; weight: 4.4-5.7 kg, *n*=7, Fooden, 1975). This suggests that male competition for access to females through direct contest competition may play an important role in driving social relationships among males and between males and females.

The reproductive seasonality of northern pig-tailed macaques remains unclear. While previous studies have categorized the species as a non-seasonal breeder (Carlson, 2011; Choudhury, 2008; Feeroz, 2003), mating and birthing peaks have been reported in Khao Yai National Park, Thailand (Carlson, 2011) and in Assam, North-East India (Choudhury, 2008), but none in Bangladesh (Feeroz, 2003). Furthermore, females display sex skin swelling and reddening during their periovulatory period (Carlson, 2011; Feeroz, 2003), which may extend their period of attractivity to the males beyond their fertile period. These results suggest that some females are likely to be simultaneously receptive, which may decrease the ability of an alpha male to control access to receptive females. Thus, further studies are needed to assess the reproductive seasonality of the species and how it affects male reproductive strategies.

Both males and females have been reported to mate promiscuously and to engage in consortships (Carlson, 2011; Feeroz, 2003). Males may engage in both single- or multiple-mount ejaculations (Carlson, 2011; Feeroz, 2003). In only one group, Carlson (2011) reported that male mating success was skewed toward the alpha-male (56% of the copulations). However, Carlson (2011), but also Feeroz (2003), indicated that all males were observed copulating with females. Females may occasionally resist a male’s copulation attempt (Carlson, 2011). They may also give post-copulation calls (Carlson, 2011), which may be used to attract other males and increase mate-guarding efforts by the consorting male (postcopulatory female choice, Maestripieri & Roney, 2005; Pradhan, Engelhardt, van Schaik, & Maestripieri, 2006). Most, if not all, of these observations come from only one group that was semi-provisioned, which in turn can affect the sociosexual behaviors of the species (Asquith, 1989). Thus, further studies on wild populations are needed to investigate male and female reproductive strategies and identify proximate factors (e.g., female reproductive synchrony, surreptitious copulations, and female mate choice) that may affect mating and reproductive distribution.

Both males and females display secondary sexual characteristics. Females exhibit sex skin reddening and swelling in the anogenital area to advertise their fertility. Results from a study of captive pig-tailed macaques showed that female’s sex skin swelling changes are correlated with estrogen and progesterone levels (Carlisle, Brenner, & Montagna, 1981). Furthermore, a correlation has also been found between the period of maximum sex skin swelling and the time of ovulation, and the number of ejaculations increased during the periovulatory phase and decreased once detumescence of the female’s sex skin swelling started (Bullock et al., 1972). Males exhibit a red line extending from the outer corner of their eye and they develop a red patch of variable form and color around the anus, with a continuous red line reaching the penis by passing in-between the ischial callosities and across and dividing the scrotum (Carlson, 2011; Oi, 1990b). However, so far, no studies have investigated the adaptive function of both male and female secondary sexual characteristics in a wild northern pig-tailed macaque population.

In summary, northern pig-tailed macaques are still poorly studied in the wild and studies on male and female reproductive strategies remain very limited (Carlson, 2011; Choudhury, 2008; Feeroz, 2003). To my knowledge, no direct measure of reproductive success (i.e., genetic paternity data) has yet been conducted to assess the relationship between male mating success, reproductive success, and dominance rank. Thus, studies are needed to evaluate under which conditions the alpha male is able or unable to monopolize female's sexual activity, if and how subordinate males may achieve sexual access to receptive females, and whether or not female mate choice plays a role in this species. Further, the adaptive function of the male's conspicuous signal remains unknown.

2.C. Study Site

The study site is located in the Mo Singto area at Khao Yai National Park (KYNP), northeastern Thailand (14°26′42″ N, 101°21′56″ E; 130 km NE of Bangkok). KYNP is part of the Dong Payayen-Khao Yai Forest Complex, which is a UNESCO World Heritage Site. Established in 1962, KYNP is the first national park of Thailand (Bartlett, 2009a) and has been the focus of ongoing primate research since 1977 (Reichard, Ganpanakngan, & Barelli, 2012). The park covers an area of 2,168 km^2 (Smitinand, 1977) and includes seasonal evergreen rainforest and grassland at an altitude from ~250 to 1,351 m above sea level (Reichard et al., 2012). The national park is home to a wide diversity of flora and fauna with around 2,000 plant species, 370 bird species, 70 reptiles and amphibians species, and 70 mammal species, including elephants, bears, gaurs, deer, and primates (Lynam, Round, & Brockelman, 2006). There are four primate species living in the park: white-handed gibbons (*Hylobates lar*), pileated gibbons (*Hylobates pileatus*), northern pig-tailed macaques (*Macaca leonina*), and Bengal slow lorises (*Nycticebus bengalensis*) (Lynam et al., 2006).

The climate of KYNP follows the Asian southwest monsoon cycle, characterized by three seasons: a rainy season with high rates of precipitation and high temperatures from May-October, a cold season marked by an absence of rain and cool temperatures from November-February, and a hot season with high humidity and temperatures from March-April (Bartlett, 2009a; Singhrattna, Rajagopalan, Kumar, & Clark, 2005). Annual precipitation ranges between 2000-3000 mm and mean monthly temperature varies between 19-24°C (Reichard et al., 2012). Food abundance is seasonally variable and can be divided into high during the months of March-September and low from October-February (Albert, Huynen, et al., 2013; Bartlett, 2009b). Data for this dissertation research were collected in the larger Mo Singto forest (Figure 2.1), which covers around 10 km^2 of tropical seasonal forest and grassland, with an altitudinal range of 730-890 m above sea level (Kitamura et al., 2005; Kitamura et al., 2008; Reichard et al., 2012; Smitinand, 1989).

2.D. Study Group

The northern-pig-tailed macaque is the only diurnal monkey at KYNP but it is commonly observed. To my knowledge, at least two northern pig-tailed macaque groups have been previously studied at KYNP. The Headquarter group (HQ group) was the first group that was studied for their post-copulatory reproductive strategies (September 2007-December 2008, Carlson, 2011) and ecology (i.e., diet, seed dispersal, sleeping sites) (April 2009-October 2010, Albert, Hambuckers, Culot, Savini, & Huynen, 2013; Albert, Huynen, et al., 2013; Albert, Savini, & Huynen, 2011). The second group, Chang (CH group), is a neighboring group to the HQ group and was studied more recently for their ecology (i.e., ranging size, territoriality, and sleeping sites) (April-May 2011, May 2012-June 2013, José-Domínguez, Asensio, García, Huynen, & Savini, 2015; José-Domínguez, Huynen, et al., 2015; José-Domínguez, Savini, & Asensio, 2015).

For this dissertation research, I focused on CH group, which was entirely wild-feeding (José-Domínguez, Huynen, et al., 2015; José-Domínguez, Savini, et al., 2015), from September 2015-June 2017. During the 22-month study, CH group comprised 60-75 individually known individuals (numbers changed during study period), including 6-10 resident males (3-5 adult males and 3-6 subadult males), 0-7 immigrant males (4 adults, 3 subadults), 18-24 adult females, and an estimated 35-45 immature individuals. The adult sex ratio ranged from 1:5 to 1:8 males to females (for further details, see Chapter 3).

This study was conducted under research permission from the National Research Council of Thailand (NRCT), the Department of National Parks, Wildlife, and Plant Conservation (DNP), and Khao Yai National Park (KYNP) in Thailand. All procedures performed in this study involving animals were in accordance with the ethical standards of the institution at which the study was conducted. This research was carried out under the Institutional Animal Care and Use Committee (IACUC) permit number 15-008 from Southern Illinois University Carbondale (SIUC).

2.E. General Overview of Methods

2.E.1. Timeline for data collection

Systematic data collection on CH group covered 22 months (September 2015-June 2017). I divided the study period into three phases. Phase I was a two-month period (September-October

2015) that was used to habituate CH group to the presence of unfamiliar researchers and identified all subadult and adult individuals of the group. Phase II was a 14-month period (November 2015-December 2016) of behavioral, morphological, and genetic data collection. Phase III covered a six-month period (January-June 2017) of bimonthly observations of the group to record births of infants who were conceived during Phase II and to collect genetic data (for further details, see 3.B.1 Study Site and Subjects).

2.E.2. Demographic records

The group composition, including birth, death, and individual emigrations and immigrations, as well as the females' parity status and the presence of extra-group males (EGMs), were recorded throughout the study period. The number and identity of adult and subadult males and adult females were recorded every day. A complete description of demographic data collection methods follows in III.B.2. Demographic Records.

2.E.3. Behavioral data collection

Throughout study Phase II, four field assistants (Chris Coll-Beswick [CC-B], Corey Bither [CB], Michelle Reed [MR], and Nik Long [NL]), and I [FT] recorded sociosexual data and male-female interactions (i.e., copulations, ejaculatory copulations, consortships, grooming, female proceptive behaviors and receptive behaviors) during females' receptive periods, using focal sampling and *ad libitum* sampling (Altmann, 1974; Martin & Bateson, 2007) (for further details, see methods in Chapters 4-6). One- to three observers collected data four- to six days a week from 7 am to 6 pm (i.e., morning to evening sleeping site). To assess male dominance rank, aggressive and submissive behaviors were recorded during focal sampling and *ad libitum* sampling (Altmann, 1974; Martin & Bateson, 2007). Male-male and female-female agonistic behaviors were used to determine male and female dominance rank (for further details, see 3.B.4. Male and Female Dominance Hierarchy). Event of rank changes, especially of take-overs of alpha male position, were recorded through *ad libitum* sampling (Altmann, 1974; Martin & Bateson, 2007).

2.E.4. Genetic paternity analysis

Genetic paternity analysis was used to assess male reproductive success measured as the number of offspring sired by a male. Between November 2015 and June 2017, 252 fecal samples were collected from 18 adult and subadult males. Fecal samples were also collected from 22 adult females of CH group, and 25 juveniles and infants. I conducted the genetic paternity analysis at the National Primate Research Center of Thailand (NPRCT) in 2016. DNA was extracted from fecal samples and then used for DNA quantification, PCR amplification, and STR genotyping.

STR genotyping was conducted on nine polymorphic human microsatellite loci by following the method described by Barelli and colleagues (2013). The maternity of the genotyped offspring was established from behavioral observations and confirmed by the genetic data, and these data helped to determine the paternity. The number of potential sires varied between nine and fifteen for the genotyped offspring born during the data collection period. The potential sires for the offspring born prior to the data collection period (i.e., born in 2014 and 2015) were assumed to be males observed during this field study and a previous field study (pers. comm., José-Domínguez). However, for these offspring, not all potential sires were known.

I used CERVUS 3.0.7 (Kalinowski, Taper, & Marshall, 2007) to assign paternity. This program determines the most likely father among a pool of potential fathers based on a computer simulation, taking into account genotyping errors and presence of close relatives in a study population (Marshall, Slate, Kruuk, & Pemberton, 1998). In addition to paternity assigned through likelihood, I also looked at the number of allelic mismatches between an offspring's genotype and potential sires' genotypes. If all potential fathers and enough markers are tested, all males, except the father, were excluded. The complete method of the genetic paternity analysis is described in IV.B.4. Genetic Paternity Analysis.

2.E.5. Male ornaments: skin coloration measurement

Hindquarter images were collected non-invasively for seven adult males (residents and EGMs), from October 2015 to November 2016, to objectively measure the red skin color exhibited by males in the anogenital area. Digital images of male subjects and a color standard (X-rite ColorChecker passport) were taken following the "sequential method," which allows the researcher to standardize images for ambient light and camera settings (Stevens, Stoddard, & Higham, 2009).

Skin reflectance modulation is determined by two blood-related dimensions, skin color and skin luminance. (Changizi, Zhang, & Shimojo, 2006; Zonios, Bykowski, & Kollias, 2001). Both of these parameters were computationally quantified to assess variation in male anogenital skin reflectance, following the method described in detail by Troscianko and Stevens (2015). Then, I used the Vorobyev-Osorio receptor noise model (Vorobyev & Osorio, 1998). This method is commonly used for comparing color and luminance in non-human visual systems to assess whether two similar signals are likely to be discriminable to the macaque visual system (Siddiqi, Cronin, Loew, Vorobyev, & Summers, 2004; Troscianko & Stevens, 2015; Vorobyev & Osorio, 1998). I followed a previously described method used in rhesus macaques (*M. mulatta*) (Higham and colleagues, 2010). For each individual, I estimated color and luminance, which represent the intensity of redness and darkness, respectively. The complete method to measure male skin color is described in VI.B.5. Assessment of Male Skin Color and Luminance.

2.E.6. Male androgen analysis

Between November 2015 and November 2016, 131 fecal samples were collected from nine adult males (resident and EGMs). Fecal samples were extracted following the method of Brown and colleagues (2005) at the Laboratory of Hormonal Analysis, Khao Khew Open Zoo, Thailand.

Microtitreplate enzyme immunoassay (EIA) was used to analyze fecal extracts for immunoreactive testosterone, using a testosterone horseradish peroxidase (HRP) conjugated label (C. Munro, UC Davis, USA) and following the method of Brown and colleagues (2005). The EIA analysis was conducted at the Laboratory of Hormonal Analysis, Khao Khew Open Zoo, Thailand. The immunoreactive testosterone includes multiple immunoreactive elements with native testosterone expected to be a minor component (Setchell, Smith, Wickings, & Knapp, 2008). Monthly levels of fecal testosterone were estimated for each individual. The complete method of the male androgen analysis is described in VI.B.4. Male Androgen Analysis.

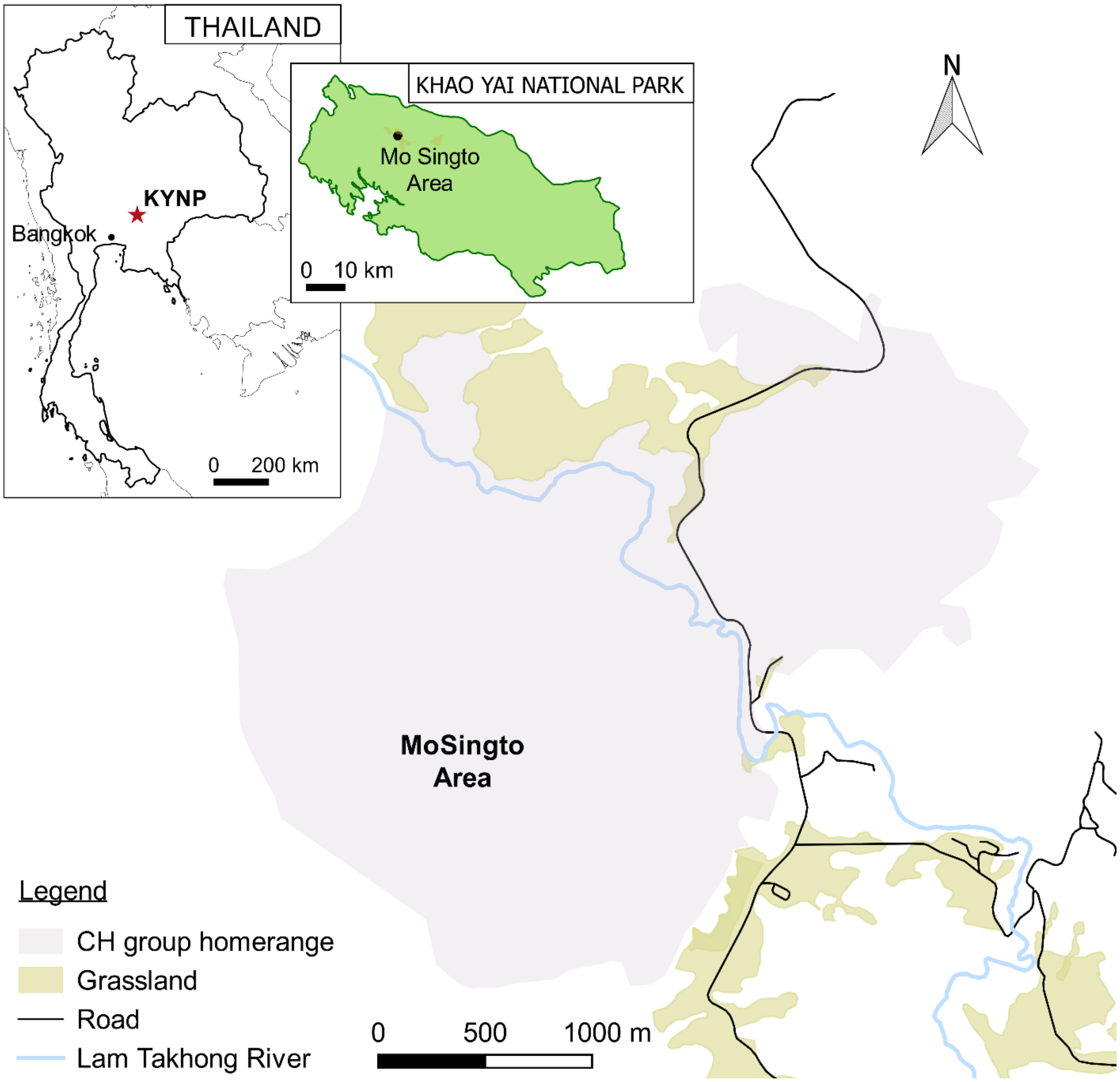


Figure 2.1 Study site and approximate home range of CH group in the Mo Singto area, Khao Yai National Park (KYNP), northeastern Thailand. The shapefile dataset, issued and modified from Sandvik (2009) and IUCN and UNEP-WCMC (2017), were used to create the Thailand's map and the KYNP's map, respectively.

CHAPTER 3

DEMOGRAPHY AND REPRODUCTIVE SEASONALITY IN WILD NORTHERN PIG-TAILED MACAQUES

3.A. Introduction

In primates, male mating strategies are determined by the competitive ability of males to monopolize receptive females, who generally are the limiting resource to male reproductive success (Darwin, 1871; Trivers, 1972). The monopolization of receptive females depends on the females' spatial and temporal distribution, and the degree of female reproductive synchrony (i.e., temporal overlap of females' receptive periods) (Setchell & Kappeler, 2003). In primates who are organized in multi-male, multi-female groups, males aggressively compete for dominance to gain preferential access to receptive females and often the top-ranking male, commonly designated the alpha-male, can enjoy the most unrestricted access to receptive females (Altmann, 1962; Cowlishaw & Dunbar, 1991). However, when more than one female is simultaneously receptive, it becomes increasingly difficult for the two-to-three top-ranking males to monopolize all receptive females during their fertile period, which often allows lower-ranking males to access those females (Altmann, 1962; Cowlishaw & Dunbar, 1991). In turn, the degree of female reproductive synchrony is affected by the number of females living in the group and the degree of reproductive seasonality of the species, which is usually a function of seasonal fluctuations in food availability (Kutsukake & Nunn, 2006; Ostner, Nunn, & Schülke, 2008; Paul, 1997, 2002).

Primate reproductive patterns are typically characterized as: 1) non-seasonal, which means sexual activity and subsequent infant births are scattered throughout the year; or 2) seasonal, which indicates that sexual activity and births usually occur within a specific period of the year or may peak in certain months of the year (Brockman & van Schaik, 2005a). Among seasonal breeders, primates can be further divided into moderately and highly/strictly seasonal breeders when 33-67% and over 67% of births occur within three months, respectively (van Schaik, van Noordwijk, & Nunn, 1999).

In non-seasonally breeding species, where usually little reproductive synchrony exists, the alpha male is expected to control most of the copulations and paternity (Alberts et al., 2006; Engelhardt et al., 2006; Setchell et al., 2005a). However, in strictly and moderately seasonally breeding species, where reproductive synchrony among females may be high, the mating and reproductive skew towards the alpha male is expected to be much more variable and often much lower compared to non-seasonally breeding species (Dubuc et al., 2011; Young, Majolo, et al., 2013). Thus, determining the degree of reproductive seasonality a species experiences is essential to understand male mating strategies and competitive regimes among males.

Among multi-male group-living primates, males' ability to control access to females depends foremost on the number of competing reproductively mature males and the stability of the male dominance hierarchy, and particularly of the strength of the alpha male (Setchell & Kappeler, 2003). The number of competing reproductively active males reflects the number of sexually mature males that are resident in a group but also of any other sexually mature males who may visit the group while females are sexually active. Visiting or extra-group males (EGMs) may be members of other multi-male, multi-female groups, may be members of an all-male band, or may live semi-solitarily (Nishida, 1966; Sprague, Suzuki, Takahashi, & Sato, 1998; Sugiyama, 1976; Sugiyama & Ohsawa, 1975, 1982). EGMs can impact the ability of resident males to control access to receptive females because these males are usually not part of the group's male dominance hierarchy, although they may successfully copulate with receptive females. An additional factor to consider when assessing males' competitive and reproductive abilities is that dominance relationships within groups can change over time. Thus, meticulously documenting any changes in dominance is required as these could potentially affect a male's expected lifetime reproductive success.

In this chapter, I describe the demography, social organization, male dominance relationships, and reproductive seasonality in one group of wild northern pig-tailed macaques (*Macaca leonina*) over a 2-year study period at Khao Yai National Park (KYNP), Thailand. The results of this chapter will be used as background data for the following chapter focusing on the male mating tactics (Chapter 4-6).

Reproductive strategies of wild northern pig-tailed macaques are still poorly understood because of the paucity of studies on wild populations (Carlson, 2011; Choudhury, 2008; Feeroz, 2003). Previous studies have reported that northern pig-tailed macaques live in large multi-male, multi-female groups with a female-biased adult sex ratio (Carlson, 2011). Even though these studies have also characterized the species as a non-seasonal breeder (Carlson, 2011; Choudhury, 2008; Feeroz, 2003), mating and birth peaks have been reported, making the question about reproductive seasonality inconclusive (Carlson, 2011; Choudhury, 2008).

Furthermore, northern pig-tailed macaques show considerable sexual dimorphism in body size and weight (Malaivijitnond et al., 2012; Smith & Jungers, 1997); thus a linear male dominance hierarchy is expected. Lastly, in one study, EGMs have been observed foraging semi-solitarily (Carlson, 2011). However, until now, no systematic observations of interactions between semi-solitary and EGMs with resident males and females of an established group are available.

3.B. Methods

3.B.1. Study site and subjects

The study site is located in the Mo Singto area in KYNP, northeastern Thailand (2,168 km^2; 14°26′42″ N, 101°21′56″ E; 130 km NE of Bangkok). The larger Mo Singto area is around 10 km^2 (José-Domínguez, Huynen, et al., 2015; Reichard et al., 2012) and is covered by a tropical seasonal forest, with an altitudinal range of 730-890 m above sea level (Kitamura et al., 2005; Kitamura et al., 2008; Reichard et al., 2012; Smitinand, 1989). KYNP can be characterized by a rainy season (May-October), a cold season (November-February), and a hot season (March-April). Food abundance is seasonally variable and can be divided into high during the months of March-September and low from October-February (Albert, Huynen, et al., 2013; Bartlett, 2009b) (for further descriptions of the study site, see 2.C. Study Site).

Systematic data collection occurred from September 2015-June 2017 on CH group, which was entirely wild-feeding (José-Domínguez, Huynen, et al., 2015; José-Domínguez, Savini, et al., 2015). I divided the study into three phases: Phase I—a two-month period (September-October 2015)—was used to identify all subadult and adult individuals of the group. Phase II—a

14-month period (November 2015-December 2016)—was the main demographic and behavioral data collection period. Phase III—a six-month period (January-June 2017) of bimonthly observation—was used to record demographic data, including births of infants who were conceived during Phase II (for further details, see 2.E.1. Timeline for Data Collection).

3.B.2. Demographic records

The group composition, including birth, death, and individual emigrations and immigrations, was recorded throughout the study period. The number and identity of adult and subadult males and adult females were recorded every day. In the following sections, further information is given on the recording method of birth events, female parity status, and male immigration status.

3.B.2.a. Record of birth events.

Data on births were recorded through daily observations during study Phases I and II. During Phase III, births were recorded at bimonthly observation intervals and estimated from the development of offspring in combination with backdating the expected period of conception based on 24 weeks of gestation (162-170 days of gestation, Chandrashekar et al., 1980). The birth months of three offspring born before the study began were estimated based on offspring development.

3.B.2.b. Female parity status.

According to the number of offspring a female had, females were divided into four parity categories: 1) nulliparous females who had never given birth to an infant; 2) primiparous females who raised only one surviving infant until the end of the study (i.e., possible abortions or stillbirths were not considered in parity evaluations) (Gomendio, 1989);

3) multiparous females who had raised more than one infant until the end of the study; and
4) females with unknown parity who had raised at least one infant, indicating that they were not nulliparous but making the distinction between primiparous or multiparous impossible.

In addition to direct observation of nursing infant, the size and morphology of a female's nipples were used as indicators of female parity status (Alviola, Duya, Duya, Heaney, & Rickart, 2011; Ransom, 1981; Ransom & Rowell, 1972). Females with consistently small nipples, suggesting that they had never given birth, were considered nulliparous (Alviola et al., 2011). Females who had small nipples before giving birth and elongated nipples after giving birth during the study, suggesting they were nursing their first infant, were considered primiparous (Alviola et al., 2011). Females who had already elongated nipples before giving birth, suggesting that they had already nursed at least one infant, were considered multiparous. "Older-looking" females (i.e., exhibiting lightening of body hair color, wrinkling of the facial skin, loosening of folds of body skin; Dittus, 1975), who did not give birth during the study but had consistently elongated nipples, were considered multiparous. Finally, females who were already nursing an infant, suggesting they could be prima- or multiparous, were considered unknown parity.

<u>3.B.2.c. Male migration status.</u> As a previous study mentioned repeated immigration and emigration of males between groups and the presence of extra-group males that could potentially copulate with females (Carlson, 2011), the presence or absence of subadult and adult males were recorded daily. Using a format adapted from van Noordwijk and van Schaik (1985), I grouped males into one of three categories:
1) Resident male: a male who has been a member of the group for at least six months, was seen daily either at the periphery or in the core area of the group, and interacted with other group

members according to dominance rank. Males who were in the group at the start of the study and who stayed for at least six months were considered resident males from the beginning of observations.

2) Immigrant male: a male who stayed in the group for at least seven days, was seen daily, often at the periphery but also in the center of the group, where he occasionally interacted with group members, showed submissive behaviors towards resident adult males, and did not provoke agonistic behaviors from adult males when being near them.

3) Extra-group male: a male who was usually seen at the periphery of the group or was absent during most observation days, rarely interacted with group members, except for receptive females, and avoided resident adult males who generally responded agonistically towards him.

3.B.3. Records of copulations

One to three observers (CC-B, CB, MR, NL, and/or FT) recorded copulations and ejaculatory copulations (see definitions in Table 4.7) using continuous focal sampling (focal sampling) (Altmann, 1974; Martin & Bateson, 2007) throughout Study Phase II (four to six days a week, 7 am-6 pm; for further details, see 2.E.3. Behavioral Data Collection). From August-December 2016, only FT collected data. Focal sampling included receptive females at one- to three-day intervals with a total of 104.2 hours in 2015 and 454.6 hours in 2016. A female was categorized as sexually receptive when she was seen mating (i.e., copulation, ejaculatory copulation, evidence of sperm plug) (Dixson, 2012; Dubuc et al., 2012). A period of female sexual receptivity (receptive period) was determined as a continuous period of mating activity over consecutive days, but it could include one-to-two days of an absence of copulation (Dubuc et al., 2012).

Focal sampling also included males (four adults, one subadult) at one- to three-day intervals with a total of 59.5 hours in 2015 and 42.3 hours in 2016 from November 2015-March 2016. From April 2016 until the end of the study, males could not be followed during the mating period as more than two females were simultaneously receptive and only these females were observed. Using a random number generator, focal individuals were chosen randomly to achieve an unbiased, equal daily observation time for each focal animal. During focal follows, all data were recorded on an iPad mini 4 using the Animal Behavior Pro iOS App (Newton-Fisher, 2012).

3.B.4. Male and female dominance hierarchy

Aggressive behaviors (bite, chase, grab, grunt, face threat, push, and scream; Maestripieri, 1999) and submissive behaviors (submissive crouch, fear grimace, flee, lip-smack, supplant/being supplanted, scream, and squeak; Caldecott, 1986; Maestripieri, 1999) were recorded during focal sampling and *ad libitum* sampling (Altmann, 1974; Martin & Bateson, 2007). Behaviors were defined as “active” when the focal animal performed them and as “passive” when the focal animal was the recipient of the behavior. Male-male and female-female agonistic behaviors were used to determine the dominance rank of resident adults and subadults (males and females).

A dominance hierarchy was established separately for each sex, using all observed dyadic interactions of aggression and submission. Bidirectional agonistic behaviors, in which two individuals aggressed each other, were considered cases of stalemate and were therefore not included in rank analyses. All dominance interactions were organized in a sociometric matrix which takes into account the identity of each opponent (winner/loser) and all their interactions (Tables 3.1-4). Linearity and steepness of the hierarchy were used as complementary measures to generate the dominance rank order and characterize male and female dominance hierarchies (de Vries, 1995; de Vries, Stevens, & Vervaecke, 2006). Indeed, primate dominance hierarchy can be categorized into dominance styles, which vary along a continuum from egalitarian to despotic based on the degree of linearity and steepness of the dominance hierarchy (de Waal, 1989). While egalitarian dominance hierarchies are defined as weakly linear and shallow, despotic dominance hierarchies are strongly linear and steep (van Schaik, 1989). The degree of linearity of each dominance hierarchy was measured via a linearity index (denoted *h'*) using a modified version of Landau's method, which is based on the variance of dominance among individuals (de Vries, 1995). The dominance hierarchy's steepness was measured via adjusted, normalized David's scores, which is based on a dyadic dominance index corrected for chance (de Vries et al., 2006).

For resident males (three to five adults and three to five subadults), I estimated three independent dominance hierarchies, corresponding each to a period of consistent social stability (i.e., periods with no rank changes). Only the subadult males (*n*=5) who engaged in agnostic interactions with adult males and copulated with receptive females were part of the dominance hierarchy calculations (see Dubuc et al., 2011). Because immigrant males and EGMs interacted infrequently with the resident males, they could not be included in CH group's male dominance hierarchy. For adult females (*n*=22), I estimated a single dominance hierarchy because female social relationships were stable and no rank changes occurred during the study.

3.B.5. Reproductive seasonality analysis

I used circular statistics to detect the degree of reproductive seasonality (Batschelet, 1981) in CH group. Circular statistics allow calculating a mean vector of length (*r*) as an index of the strength of the seasonality signal of a data set to describe objectively and to compare the temporal spread of reproductive events (Janson & Verdolin, 2005; Xiang et al., 2017). Vector length (*r*) is a measure of how closely spaced observations of mating or birthing events are in relation to a circular axis (across an annual cycle) (Janson & Verdolin, 2005). Values for *r* range from zero to one, with zero indicating that events are evenly spread around a circular axis, and one indicating that events are closely clustered in one place (i.e., a month) on the circular axis (Batschelet, 1981; Janson & Verdolin, 2005).

Circular statistics can be applied to data that involve time continuity and recurrent seasonality and can be represented as a circle of angles (Batschelet, 1981). To describe birth and mating seasonality, the total length of the circular axis is the year, divided into 12 sectors (equivalent to the 12 months of the year), and each sector is 360˚/12 (e.g., January is 30˚). Each observation is converted as a vector of length one and an angle given by the month of observation. All vectors are summed to a single vector of total length L and angle α (Batschelet, 1981; Janson & Verdolin, 2005). The mean vector length (*r*) is calculated by dividing the total length L of the single vector by the number of observations.

An Omnibus test for grouped data (Pewsey, 2002) was used to test if mating and birthing showed evidence of significant seasonal variation. The Omnibus test tests the null-hypothesis of a uniform distribution of events against all alternatives. As recommended by Pewsey and colleagues (2002), I chose an Omnibus test instead of the generally applied Rayleigh test because data of birth events and mating were recorded as monthly totals along a 12-month scale (i.e., as mutually exclusive categories). From the entire data set, I used two full years of monthly birth frequencies (June 2015-May 2017) and one complete year of monthly copulation frequencies (November 2015-October 2016) to have an even multiple of 12 months.

3.B.6. Statistics

I used the package "steepness" (Leiva & de Vries, 2014) to generate the rank order and to test the steepness of the dominance hierarchies of males and females. The package "compete" (Curley, 2016) was used to calculate the corrected Landau index of linearity of rank relationships (de Vries, 1995). The package "circular" (Agostinelli & Lund, 2017) was used to run Omnibus tests. All statistical analyses were performed in R v. 3.5.1 statistical software package (R Development Core Team, 2018).

3.C. Results

3.C.1. Demographic records

3.C.1.a. General composition of CH group. From September 2015-June 2017, CH group varied between 60 and 75 individuals. There were 6-10 resident males (3-5 adult males and 3-6 subadult males), 0-7 immigrant males (4 adults, 3 subadults), 18-24 adult females, and an estimated 35-45 immature individuals (Figure 3.1). The adult sex ratio ranged from 1:5 to 1:8 males to females. A total of 22 births were recorded between June 2015 and May 2017.

3.C.1.b. Adult female's parity status. During the study period, 24 adult females were members of CH group and were categorized according to their parity status as follow: 1) three nulliparous females who gave birth during the study and became primiparous; 2) thirteen multiparous females; and 3) eight females with unknown parity, of which six definitively became multiparous after giving birth. Additionally, six adult females disappeared from the group and may have died, but no bodies were found. Seventeen live births and three stillbirths were recorded (Figure 3.1).

3.C.1.c. Ting's death. Adult male Ting, who had been the alpha male of CH group at the study onset until March 2016, died on October 20, 2016 (two months before the end of study Phase II). He fell from a branch of less than five meters high and remained on the ground until he died a few hours later. He had blood and white foam running from his mouth and nose, his body was convulsing, and he had apparent difficulties breathing while several group members around him were giving snake-typical alarm calls. His arms and legs appeared paralyzed and his lower body showed some signs of strangulation. Although the cause of death is not conclusive, several symptoms and circumstances are in agreement with a snake attack. It appeared likely that he fell victim to the bite of a venomous snake or he may have been strangled by a reticulated python, which are common at the site.

3.C.1.d. Extra-group males. Observations of 14 EGMs (11 adults, 3 subadults) in CH group's vicinity were scattered throughout the study period (Figure 3.1). EGMs were never seen to be part of another multi-male, multi-female group or an all-male band because all-male bands were not witnessed. EGMs were usually encountered foraging on their own. At the periphery of CH group, EGMs were present for a few days to more than a month with intermittent gaps of one- to three days when the group was not observed. Brief observation interruptions could have been due to my field observation schedule, which included days off the field (used for data entry, errand run, and break), but EGMs may have also been unnoticed by the observers or EGMs may have been in fact not present in the group's periphery.

3.C.1.e. Immigration and emigration records of CH group's males Among EGMs observed at the periphery of CH group, five adult males, Farang, Khao, Ram, Mii, and Aran, immigrated into CH group. Farang immigrated in October 2015, stayed for two months, and took over the alpha male position in the male dominance hierarchy for about a week in December 2015 before his disappearance after December 22nd (see below 3.C.3.a. Take-over by Farang in December 2015). Khao immigrated into CH group in March 2016 but stayed only for one week. He immigrated again into the group in April 2016 when he took over the alpha male position and remained as a resident until the end of the study in June 2017 (see below 3.C.3.b. Take-over by Khao in April 2016).

The three other males, Ram, Mii, and Aran, immigrated into CH group without challenging the alpha male for dominance. Ram immigrated in January 2015, stayed for two months as an immigrant male, and emigrated at the end of February 2016. Ram was seen again for less than a week in March 2016 as an EGM at the periphery of the group. Mii immigrated in March 2016, stayed for three weeks as an immigrant male, and emigrated at the beginning of April 2016 when Khao took over the alpha male position. Mii was seen again in CH group as an immigrant male for one week in June 2016 and as an EGM for less than a week in August 2016. Aran immigrated in October 2016, stayed for one month as an immigrant male, and emigrated at the end of November 2016.

Three subadult males, Randy, Juno, and Mu, immigrated into CH group in January, June, and October 2016, respectively. Randy and Mu remained in the group until the end of the study in June 2017 and were considered resident males in August 2016 and April 2017, respectively. Juno emigrated from the group at the end of November 2016, which coincided with the emigration of subadult males Chaa and Toy who were residents of the group since the start of the study in September 2015. The fate of the latter three subadults remained unknown.

3.C.2. Dominance hierarchy

3.C.2.a. Male dominance hierarchy. I witnessed two male take-overs of the alpha male position, each by an immigrant male. The first take-over occurred in December 2015 when immigrant male Farang ousted the alpha male Ting (rank change Ting-Farang), who had been the top-ranking male since 2012 (pers. comm., José-Domínguez) but remained in the group as the beta male. However, Farang disappeared about a week after he had attained the alpha male position and Ting regained the alpha male position after Farang's disappearance (rank change Farang-Ting). The second take-over occurred in April 2016, when Khao immigrated and replaced alpha male Ting (rank change Ting-Khao).

Both take-overs of dominance occurred in less than six months and the challenging males were fully-grown, young prime males (i.e., full adult size, sharp canine, large crown hair on top of the head, and "healthy-looking" coat of body hair). The age of Ting was not known, but his physical appearance indicated that he was probably a post-prime male (i.e., healthy adult exhibiting some lightening of body hair color, more wrinkling of facial skin, more body scars, and more erosion and tartarization of the teeth than young prime males). Ting had held the alpha male position of CH group for four years (since 2012 when he took over the alpha position, pers. comm., José-Domínguez). After losing his alpha male position in April 2016, Ting went down to the third-ranking position and died seven months later from a supposed snake attack (see above 3.C.1.c. Ting's death).

Because periods of take-overs must be considered situations of great social disruption, I estimated three dominance hierarchies, one for each period of social stability following each change of the alpha male position (Tables 3.1-3). With three to four adult males resident in the group at any time, the first dominance hierarchy (three adult and three subadult males) had adult male dominance rank Ting-Snoopy-Kanhuh for the first six months (Oct. 2015-Mar. 2016), excluding the one-week period when Farang took over the alpha male position. The second dominance hierarchy (four adult and three subadult males) was established for the one-week period of takeover by Farang in December 2015 with adult male dominance rank Farang-Ting-Snoopy-Kanhuh. Finally, the third dominance hierarchy (three to four adult and three to five subadult males) was established for the remaining 15 months (Apr. 2016-Jun. 2017) with adult male dominance rank Khao-Snoopy-Ting-Kanhuh.

Overall, Snoopy maintained the same position as beta male throughout the study period, except during the one-week period when Farang was the alpha male and Snoopy went down to the third-ranking position. Kanhuh's dominance position varied between third and fourth rank. The five subadult males had the lowest-ranking positions and their dominance rank were stable throughout the study period but fluctuated according to the change of rank among adult males.

The male dominance hierarchies were strongly linear and steep during the three periods (Oct. 15-Mar. 16: h'=1, p=0.024; *steepness*=0.69, p<0.001; Dec. 15: h'=1, p=0.039; *steepness*=0.60, p<0.001; Apr. 16-Jun. 17: h'=0.91, p<0.001; *steepness*=0.57, p<0.001). The male dominance hierarchy was steeper during the period Oct. 2015-Mar. 2016 (with Ting as the alpha male) than the two other periods with either Farang or Khao as alpha males.

Immigrant males and EGMs could not be included in the dominance hierarchy due to their limited interactions with the rest of the group and their non-continuous presence in the group.

Nonetheless, on those rare occasions when they interacted with resident males, immigrant males and EGMs displayed submissive behaviors towards resident males. Further, all EGMs who migrated into the group started as low-ranking males. However, there were a few exceptions. Farang and Khao both immediately took over the alpha male position, and one of the EGMs, adult male Chuan (observed occasionally during the three-month mating peak of 2016), displayed dominant behaviors towards resident males during a consortship with a receptive female (see also Chapter 5).

3.C.2.b. Female dominance hierarchy The female dominance hierarchy was divided into three rank categories: high-ranking females (ranks 1-7), middle-ranking females (ranks 8-16), and lower-ranking females (ranks 17-22). Two females, Gamonh and Miou, were not assigned a dominance rank because they were only observed on a few occasions in the vicinity of the group before they disappear and no interactions with other resident females were recorded. Although the females formed a linear dominance hierarchy like the males, their hierarchy was weaker and shallower from October 2015 to June 2017 (h'=0.35, p<0.001; *steepness*=0.24, p<0.001; Table 3.4), probably because interactions among females more often remained unresolved than among males, particularly among lower-ranking females.

3.C.3. Take-overs of male dominance

Take-overs are rare events that have scarcely been documented in the wild, thus descriptive information as reported below provides insight into a rarely witnessed aspect of northern pig-tailed macaque society and primate society in general. In this section, I provide details of two male take-over events (rank change Ting-Farang and rank change Ting-Khao) that I observed in CH group during the study period (Figure 3.1).

3.C.3.a. Take-over of dominance by Farang in December 2015. Farang was a young, fully-grown adult EGM, observed occasionally at the periphery of the group when the study began in September 2015. From October 2015 onwards, he followed CH permanently and began interacting more frequently with resident subadults and juveniles (presenting, grooming). From December 14-22, 2015, Farang challenged alpha male Ting and was dominant over Ting for approximately one week before disappearing. His fate remains unknown.

Details of the take-over of dominance by Farang are provided as excerpts from field notes:

- December 13th: CH group was stable and Farang, who appeared to have been integrated into the group as a new immigrant male, because he has been seen to groom and present to resident subadult and juvenile males, showed no agonistic behaviors towards the other group males.
- December 14th-16th: No observer with CH group; Farang was assumed to have started challenging the alpha male Ting during this time.
- December 17th: Farang was found with several injuries at 11:00. He was limping and his left leg was covered in blood. His right hand was swollen with a shallow bite wound to the palm. He was seen in the middle of CH group, while former alpha male Ting and former beta male Snoopy, who both had suffered bites to their faces, stayed at the periphery of the group. Subordinate adult male Kanhuh was not seen all day and young adult male, Khao, was seen for the first time with the group. Despite his injuries, Farang followed and copulated with two receptive females. No interactions were seen between the resident adult males and Farang, but

resident subadult males and adult females showed submissive and avoidance behaviors towards Farang.

- December 18th: Around 09:30, Ting and Snoopy formed an alliance and started challenging Farang while on the ground. Direct agonistic contacts were limited, and Ting and Snoopy mainly screamed at Farang. Other group members likewise screamed and acted highly agitated. Farang, at least once, attacked Snoopy and bit him, whereupon Snoopy ran out of Farang's sight and the challenge ended. Ting remained around Farang and displayed submissive behaviors. Later after 16:00, Ting and Snoopy, who had returned by 15:00 in the group, occasionally behaved submissively towards Farang. Farang copulated with one receptive female. Kanhuh and Khao were absent from the group.
- December 19th-20th: No fighting was observed, only occasional squabbling (i.e., low-intensity agonistic behaviors such as grunting, growling, and brief chases) were recorded between Farang and the other resident males. These agonistic behaviors seemed mostly to establish Farang's dominant position. Ting, Snoopy, and subadult males occasionally stayed around Farang, but mostly avoided his presence. Farang, Ting, Snoopy, and subadult male Naam engaged in copulations with three receptive females. Khao was seen at the periphery but Kanhuh remained absent.
- December 21st: Around 9:30, a severe fight broke out. It only lasted ~4 min, but left several males injured and the group agitated (screaming, excited grunts, running, jumping) for another 30 minutes. Kanhuh had returned to the group. Fighting started when Kanhuh and Snoopy approached the main party of the group moving towards Farang and Ting, while Kanhuh was growling. The six males, Ting, Snoopy, Kanhuh, Naam, Chaa, and Toy, began screaming and then launched an attack against Farang with direct body contact. Farang severely bit Kanhuh,

which increased the intensity of the fight, involving more biting. Farang left the fight most seriously injured, with a deep cut to his face and a severe wound to his left leg leaving muscle tissue exposed (Figure 3.2). Ting had a deep, long open wound under his arm and another on his back (Figure 3.3). Snoopy appeared to have just a few superficial skin cuts. Kanhuh was limping, although the wound he had received was not readily visible. Juveniles and several adult females had also joined in the fight and had been observed screaming and growling at Farang. And it appeared likely from the overall interaction pattern that some of them may also have bitten or tried to bite Farang. No additional fighting was observed until the end of the observation day, and Ting behaved submissively to Farang's threats. Other group members likewise showed submissive behaviors towards Farang. Only subadult male Naam was observed to copulate with two receptive females, while the other adult males seemed to ignore these instances and spent most of the remaining day foraging, resting, or tending their wounds. Snoopy and Kanhuh left in the afternoon.

- December 22nd: Farang spent most of the day at the periphery of the group and only few submissive behaviors were noticed from other males. Farang often licked his still wide-open injuries. Ting also tended his wounds although his wounds appeared less severe. Only the subadult males copulated with the receptive females, while Ting and Farang were not seen mating. Khao was observed near a receptive female at the end of the day, but he was chased away from the female by Naam and Ting. Snoopy and Kanhuh were not seen the entire day. However, on their way back to the field station house, field assistants CC-B and CB encountered Kanhuh, approximately 3 km away from the group, traveling by himself along the river.
- December 23rd: When the group was found at 07:25, only Ting and the three subadult males were found with the group. No sexual activity (i.e., copulation or consortship) with females

exhibiting sex skin swelling was recorded. Ting was however seen grooming with adult females including females exhibiting sex skin swelling.

- December 24th: Snoopy and Kanhuh were found in the main party of the group with Ting at 08:20, and both males behaved submissively towards Ting. Khao was observed once at the periphery of the group. No mating was observed.

The disappearance of Farang after December 22nd remained unexplained, and although no body was found, it seems possible that he died from his serious injuries. The temporary change of dominance between Farang and Ting lasted approximately one week (6-9 days).

<u>3.C.3.b. Take-over of dominance by Khao in April 2016.</u> Khao was a young, fully-grown adult EGM of unknown origin, who was first spotted with CH on December 17, 2015. On December 24, 2015, he was not seen with the group, coinciding with Farang's disappearance. Khao immigrated into CH group on March 2, 2016, but he was not seen with the group anymore after March 9, 2016. Since his full integration in early March, he was tolerated by the resident males including the dominant male Ting in the main party of the group without provoking agonistic behaviors. Khao was seen to groom adult female Vicky and juveniles. From March 10th until April 3rd (24 days), Khao was absent from the group. Upon his return on April 4th, Khao challenged Ting and successfully took over the alpha male position in the male dominance hierarchy.

Details of the take-over of dominance by Khao are provided as excerpts from field notes below:

- April 4th: At dawn at 06:45, the group was very agitated and scattered. Different individuals were screaming and growling. Khao was in the middle of the group on the ground with fresh blood dried up on his right leg from a deep cut. The resident males are growling up in the trees. Around 08:00, Kanhuh came down to the ground from a feeding tree. Khao followed and growled at Kanhuh, who growled and loudly screamed back at Khao. Ting and Snoopy immediately came down from the feeding tree and approached Khao while growling. The three resident males attacked Khao with direct contact including severe bites. No other resident individuals were involved in the fight. A few minutes later when the fight was over, Snoopy and Kanhuh ran away, out of sight of Khao. Ting went up in a tree and cleaned a deep, large, bleeding head wound with his hands (Figure 3.4). Khao cleaned a bleeding injury on his rump from Kanhuh's bite. Then, Khao went up in a tree to forage, but Ting, Snoopy, and Kanhuh could no longer be seen. Around 9:45, a new fight broke out provoked by Kanhuh, who approached and growled at Khao. Khao growled back. Ting and Snoopy immediately approached and the three resident adult males again attacked and bit Khao. While fighting, the three resident males displayed aggressive behaviors (bite, grab, face threat, push, and scream) and submissive behaviors (fear grimace and lip-smacking) at the same time. Subadult males and several adult females and juveniles were also seen screaming and growling at Khao, and few of them bit him. The fight lasted less than 2 minutes after which Ting, Snoopy, and Kanhuh ran away and disappeared for most of the day. Khao remained in the central party of the group around the adult females who displayed submissive behaviors towards him. The adult male Mii, who had immigrated into the group in March 2015, stayed away from all agonistic interactions between Khao and the resident males and emigrated from the group the day after.

- April 5th: No observer with CH group.
- April 6th: In the morning, the group was contacted at 06:50. Snoopy avoided Khao who was foraging in the vicinity of the adult females. The resident males stayed away from Khao. Around

11:20, Khao approached Snoopy who immediately fled and displayed submissive behaviors (fear grimace and lip-smacking) in a distance. Then, Kanhuh approached in sight of Khao and started growling at him. Ting followed Kanhuh. Kanhuh and Ting approached and started fighting with Khao. Juvenile males and several adult females were also seen screaming and growling at Khao, and a few of them may have bitten him. Then, Snoopy approached and chased away Kanhuh. Once the fighting stopped, Ting displayed submissive behaviors (fear grimace and lip-smacking) towards Khao and other individuals around stopped screaming. Snoopy stayed within about 10 m of Khao and both males started to forage. For the rest of the day, Khao was seen foraging with the central party of the group. The other resident males were seen occasionally around Khao and all showed submissive behaviors towards him. Snoopy, however, showed few dominant behaviors (chase, face-threat, and grunt) towards Ting, which had never been observed before. This was the first evidence that Snoopy had become Khao's ally and was supporting Khao against former alpha male Ting, who seemed to have dropped to the third-ranking position since Snoopy appeared to dominate him.

- April 7th: Khao and Snoopy were present; no fighting was recorded. Ting and Kanhuh remained absent all day, and Snoopy was seen foraging in sight of Khao and displayed submissive behaviors towards him.
- April 8th-22nd: No observer with CH group.
- April 23rd: The four resident males Khao, Snoopy, Ting, and Kanhuh were present in the group. No injuries were detected any longer. Based on dominant/submissive behaviors, Khao was still the alpha male and Snoopy had kept his position of beta male. Ting was now third-ranking as he showed submissive behaviors towards both, Khao and Snoopy, but was able to solicit submissive behavior from Kanhuh, who was now the lowest-ranking male.

In less than 20 days, Khao successfully took over the dominance of the group, replacing Ting, who was not ousted from the group by Khao. Ting remained in the group as a third-ranking male. Snoopy maintained the same dominance position as beta male. Kanhuh went down to the fourth-ranking position. For the next 15 months, when the study ended, no further dominance rank changes were noted.

3.C.4. Reproductive seasonality

Fifteen adult females (63%) gave birth to 22 infants, between June 2015-May 2017 (Figure 3.5). Nineteen infants lived, but three were stillborn. The distribution of births in different calendar months deviated significantly from a random distribution (Omnibus test, U_G^2=0.247, p=0.014) with a mean vector (r) length of 0.432, which measured how closely spaced birth observations were made across the year. More than 80% of births (n=19) occurred between January-June (6 months), with two birth peaks in January-February and May-June, representing 31.8% (n=7) and 36.4% (n=8) of births, respectively (Figure 3.5). Only one birth each occurred in July and August and an isolated stillbirth was noted in November, but the baby’s body appeared premature and was smaller in size than regular newborns.

Thirteen females engaged in 563 copulations from November 2015-October 2016. The monthly distribution of matings differed significantly from random (Omnibus test, U_G^2=0.247, p<0.001), and was concentrated in the months of June-December with 90.6% of copulations (n=510) and a mean vector (r) length at 0.424 (Figure 3.6). A mating peak occurred in July-September that included 55.1% of copulations (n=310), and nearly 25% of copulations (n=136) occurred in August alone. A smaller mating peak was observed in December with 16.7% of copulations (*n*=94), and isolated copulations of a single adult female who had a stillbirth in November were recorded in February (3.9%, *n*=22) and March (5.5%, *n*=31).

3.D. Discussion

This study provides basic descriptive information on the social organization, demography, and reproductive seasonality of one group of wild northern pig-tailed macaques in KYNP, Thailand. With a relatively large multi-male, multi-female composition with a female-biased adult sex ratio, the social organization of my study group was similar to those found in other studies of the same species and also of other macaque species (i.e., southern pig-tailed macaques, *M. nemestrina*, long-tailed macaques, *M. fascicularis,* stump-tailed macaques, *M. arctoides,* reviewed by Thierry, 2011). During the study period, CH group varied between 60-75 individuals and was composed of 3-5 adult males, 3-6 subadult males, 0-7 immigrant males, 18-24 adult females, and an estimated 35-45 immature individuals. The group size of northern pig-tailed macaques at KYNP (CH group, this study; HQ group: 53-59 individuals, Carlson, 2011) was higher than any other group of this species observed so far in the wild (e.g., seven groups, Assam, India: 16-33 individuals, Choudhury, 2008). Further, the adult sex ratio of CH group was higher (1:5 to 1:8, this study) than any other groups observed in the wild (1:2 to 1:3, Carlson, 2011; 1:5.5, Choudhury, 2008). These results indicate a wide range of group size and composition for this species. In closely related southern pig-tailed macaques, a correspondingly wide variation in group size (15-81 individuals) and sex ratio among adults (1:3 to 1:12) has also been found (Caldecott, 1986; Oi, 1996). The larger group size observed at KYNP could be related to food availability but KYNP has been characterized by a relatively depauperate fauna

(Lynam et al., 2006). Indeed, at KYNP, there are only four primate species, whereas in other comparable habitats (i.e., around the same latitude), there are usually 7-12 primate species (e.g., 8 primate species at Cát Tiên National Park, Vietnam; 12 at Hin Namno National Biodiversity Conservation, Laos; reviewed by Hassel-Finnegan, 2009). Thus, a particularly "rich" ecological setting seems unlikely, although it cannot be excluded. Another possible explanation for the larger group size of northern pig-tailed macaques observed at KYNP is the relative lack of competition from other primate species.

Interestingly, while no all-male bands were observed, EGMs were often observed in the vicinity of CH group throughout the study period. In many populations of Japanese macaques (*M. fuscata*), extra-group males have been identified as semi-solitary males visiting bisexual groups during the mating season (Nishida, 1966; Sugiyama, 1976; Sugiyama & Ohsawa, 1975, 1982). However, their status remains ambiguous because those males may forage alone, may join all-males groups, or may join bisexual groups during the non-mating season (Nishida, 1966; Sprague et al., 1998; Sugiyama, 1976; Sugiyama & Ohsawa, 1975, 1982). Furthermore, outside the mating season, semi-solitary males who foraged alone continued to interact at different levels with social group members, ranging from 0-51% of observation time (Sprague et al., 1998). In my study, such analysis could not be conducted because EGMs were impossible to follow once they left the vicinity of CH group.

Migration of EGMs Farang, Ram, Mii, Khao, and Aran as low-ranking males into the group were observed. Among these immigrants, I identified two types: 1) males who immigrated into the group at a low rank and who did not copulate with receptive females or attempt to take over the alpha male position (Ram, Mii, and Aran); and 2) males who attempted to take over the dominance of the group (Farang, and Khao). In the latter type 2, the male either: 2a) immigrated in the group for a few months and remained at a low rank in the male dominance hierarchy before attempting to take over the dominance (Farang); or 2b) visited the group several times before attempting to directly take over the dominance of the group without prior immigration into the group (Khao). The first type of immigrants is similar to “unobtrusive” males, while the second type would fall into the category of “bluff” males described by van Noordwijk and van Schaik (1985) in long-tailed macaques (*M. fascicularis*). In my study, Farang and Khao, who at different times attempted and successfully took over the alpha male position, were prime young adult males, resembling the “bluff” male types described as being young adult males only (van Noordwijk & van Schaik, 1985). My data sample remains too small to determine whether “unobtrusive” and “bluff” male types are typical and found in other social groups of northern pig-tailed macaques and whether the pattern is age-related. However, the observations of two attempts to take over the dominance rank indicate that males are forced to acquire higher rank through agonistic behaviors upon entering a group. Acquiring dominance through force has also been documented in southern pig-tailed macaques (Oi, 1990a), long-tailed macaques (van Noordwijk & van Schaik, 1985), and crested macaques (*M. nigra*, Marty, 2015).

Previously, evidence for reproductive seasonality in northern pig-tailed macaques was unclear. In my study, mating and births recorded in one group of wild northern pig-tailed macaques differed significantly from a random distribution. When comparing the birth vector (*r*) calculated in this study to other primate species, northern pig-tailed macaques from CH group are characteristic of a primate species with most births occurring over a concise six-month period (Janson & Verdolin, 2005). Indeed, all 22 births, except one, occurred from January to August with two higher peaks in January-February and May-June. Similarly, all births occurred over a discrete period of time, around the same time of the year, in the semi-provisioned HQ group in

KYNP, Thailand (January-July, Carlson, 2011) and in wild groups in Assam, India (January-May, Choudhury, 2008). Those two studies and this study also included a three-month period when 33-67% of births occurred. This set of results fits the definition of a moderately seasonal breeder (see van Schaik et al., 1999). Furthermore, data are in line with the mating distribution observed in CH group where 90.6% of the matings occurred between June-December with two higher peaks in July-September and in December (this study). The mating and birth vectors (*r*) calculated in this study were similar. Based on the comparative analysis of primate reproductive seasonality of van Schaik and colleagues (1999), I suggest that northern pig-tailed macaques, at least in this group, should be categorized as moderately seasonal breeders.

However, nuances to this classification across different northern pig-tailed populations need to be acknowledged. Year-round births were recorded except for one month in five wild northern pig-tailed macaque groups in Bangladesh (Feeroz, 2003). Year-round mating was also observed in HQ group in KYNP (Carlson, 2011), and differences of monthly birth patterns between both years of the study were detected in CH group in KYNP (this study). These results clearly suggest that northern pig-tailed macaques are not obligatory seasonal breeders but that their patterns of reproduction are flexible and their degree of seasonality are variable and may be season dependent. They may adapt their patterns of reproduction to changing cycles of food availability depending on seasonality and year-to-year variation (see Brockman & van Schaik, 2005a). Thus, the degree to which births and matings are clustered to some months of the year may vary from year-to-year. Further studies from other groups in different habitats and latitudes are much needed to better characterize the reproductive seasonality and the ecological factors which may affect it in northern pig-tailed macaques.

Table 3.1 Dominance matrices for adult and subadult males of CH group during the period October 2015-March 2016 with Ting as alpha male. The winners of aggressive interactions and the receivers of submissive behaviors are in the left hand column, and the losers of the aggressive interactions and the individuals who displayed submissive behaviors are in the top row.

		Subadult males			**Adult males**		
		Toy	Chaa	Naam	Kanhuh	Snoopy	Ting
Subadult males	Toy	NA	0	0	0	0	0
	Chaa	1	NA	0	0	0	0
	Naam	4	3	NA	0	0	0
Adult males	Kanhuh	1	1	4	NA	0	0
	Snoopy	2	2	3	6	NA	0
	Ting	3	2	2	10	5	NA

Table 3.2 Dominance matrices for adult and subadult males of CH group during the one-week period of take-over by Farang. The winners of aggressive interactions and the receivers of submissive behaviors are in the left hand column, and the losers of the aggressive interactions and the individuals who displayed submissive behaviors are in the top row.

		Subadult males			**Adult males**			
		Toy	Chaa	Naam	Kanhuh	Snoopy	Ting	Farang
Subadult males	Toy	NA	0	0	0	0	0	0
	Chaa	0	NA	0	0	0	0	0
	Naam	1	1	NA	0	0	0	0
Adult males	Kanhuh	0	0	1	NA	0	0	0
	Snoopy	1	1	1	1	NA	0	0
	Ting	0	0	1	1	1	NA	0
	Farang	2	1	2	1	4	4	NA

Table 3.3 Dominance matrices for adult and subadult males of CH group during the period April-June 2017 with Khao as alpha male. The winners of aggressive interactions and the receivers of submissive behaviors are in the left hand column, and the losers of the aggressive interactions and the individuals who displayed submissive behaviors are in the top row.

		Subadult males					**Adult males**			
		Randy	Juno	Toy	Chaa	Naam	Kanhuh	Ting	Snoopy	Khao
Subadult males	Randy	NA	0	0	0	0	0	0	0	0
	Juno	2	NA	0	0	0	0	0	0	0
	Toy	1	2	NA	0	0	0	0	0	0
	Chaa	1	1	1	NA	0	0	0	0	0
	Naam	2	3	2	2	NA	0	0	0	0
Adult males	Kanhuh	1	1	2	0	8	NA	0	0	0
	Ting	2	2	1	0	1	14	NA	0	0
	Snoopy	3	2	2	4	1	9	14	NA	0
	Khao	2	2	1	0	2	22	12	19	NA

Table 3.4 Dominance matrices for adult females of CH group during the period October 2015-June 2017. The winners of aggressive interactions and the receivers of submissive behaviors are in the left hand column, and the losers of the aggressive interactions and the individuals who displayed submissive behaviors are in the top row.

	Kay	Wat	Lawan	Tao	Alyssa	Olan	Som	Em	Ice	Muay	Fon	Dam	Baan	Hong	Jambee	Lek	Vicky	Mulan	Chompoo	San	Paapai	Jenny
Kay	NA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Wat	0	NA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lawan	1	0	NA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tao	0	1	1	NA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alyssa	2	4	0	1	NA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Olan	2	3	4	0	3	NA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Som	0	0	0	0	0	0	NA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Em	2	0	0	1	2	2	0	NA	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Ice	0	0	0	0	0	0	2	2	NA	0	0	0	0	0	0	0	0	0	0	0	0	0
Muay	0	0	2	0	6	1	1	4	2	NA	0	0	0	0	0	0	0	0	0	1	0	0
Fon	1	2	0	0	0	0	0	2	0	2	NA	1	0	0	0	0	0	0	0	0	0	0
Dam	6	1	0	0	4	3	0	5	4	9	2	NA	0	1	0	0	0	0	0	2	0	0
Baan	1	3	0	0	3	1	0	3	0	3	1	1	NA	0	0	0	0	0	0	0	0	0
Hong	0	1	6	0	6	2	0	0	2	4	4	11	1	NA	0	1	0	0	0	0	0	0
Jambee	0	3	1	0	0	0	0	4	0	6	3	6	0	1	NA	0	0	0	0	0	0	0
Lek	1	0	0	0	0	0	0	2	0	2	1	0	1	2	3	NA	0	0	0	0	0	0
Vicky	0	0	2	0	0	0	1	1	0	0	2	0	1	2	3	2	NA	0	0	0	0	0
Mulan	3	1	0	1	0	1	2	3	1	0	2	1	1	3	2	1	0	NA	0	0	0	0
Chompoo	5	0	1	0	3	1	0	5	4	2	3	6	0	3	8	4	6	5	NA	0	0	0
San	0	1	0	0	2	0	1	1	1	3	0	3	0	0	4	2	5	3	7	NA	0	0
Paapai	1	0	0	0	0	0	0	1	2	1	0	1	0	0	1	0	2	0	0	3	NA	0
Jenny	0	0	0	0	3	1	2	0	0	0	0	1	1	0	1	1	3	4	3	13	2	NA

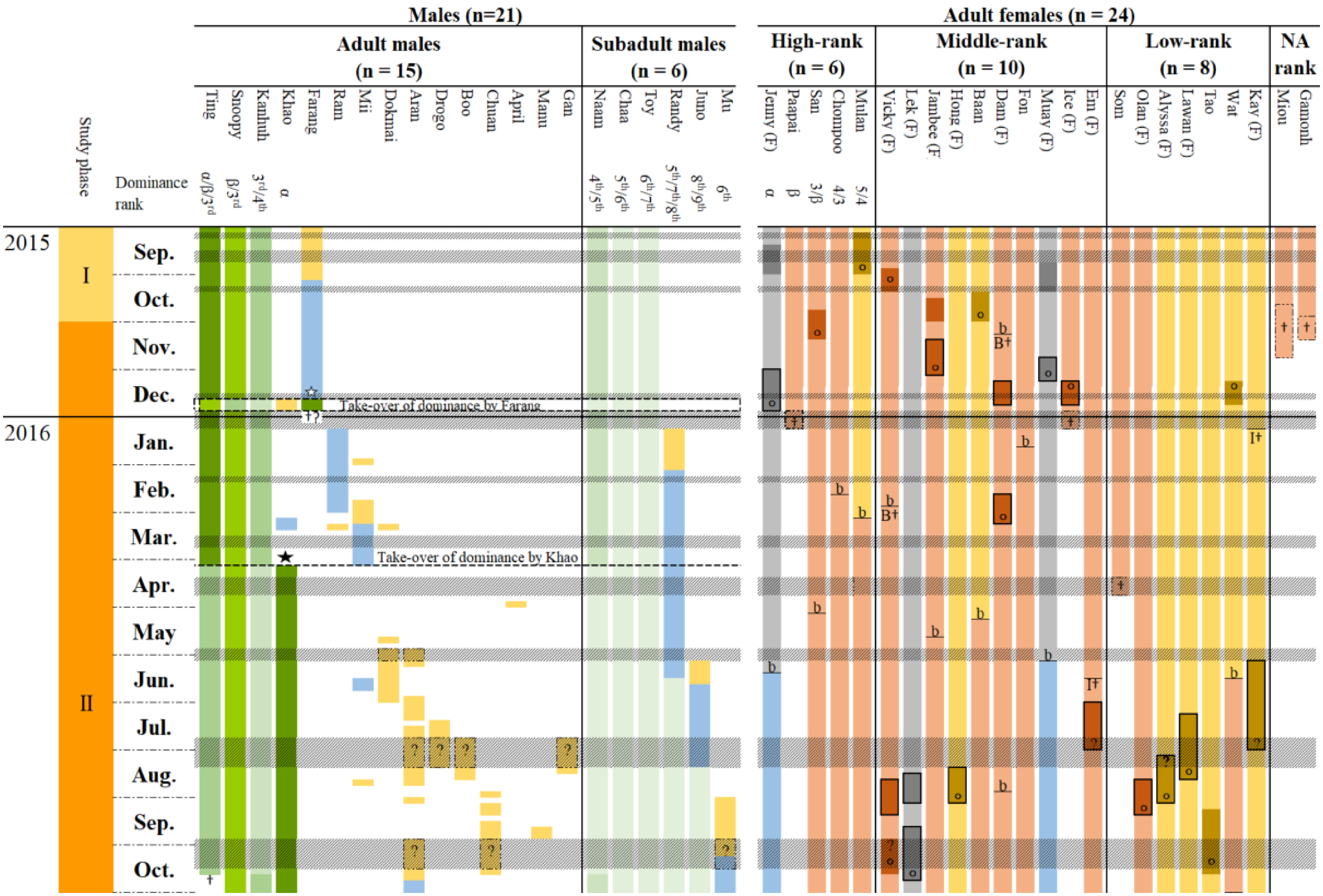


Figure 3.1 Demography of CH group from September 2015 to June 2017 at Khao Yai National Park, Thailand.

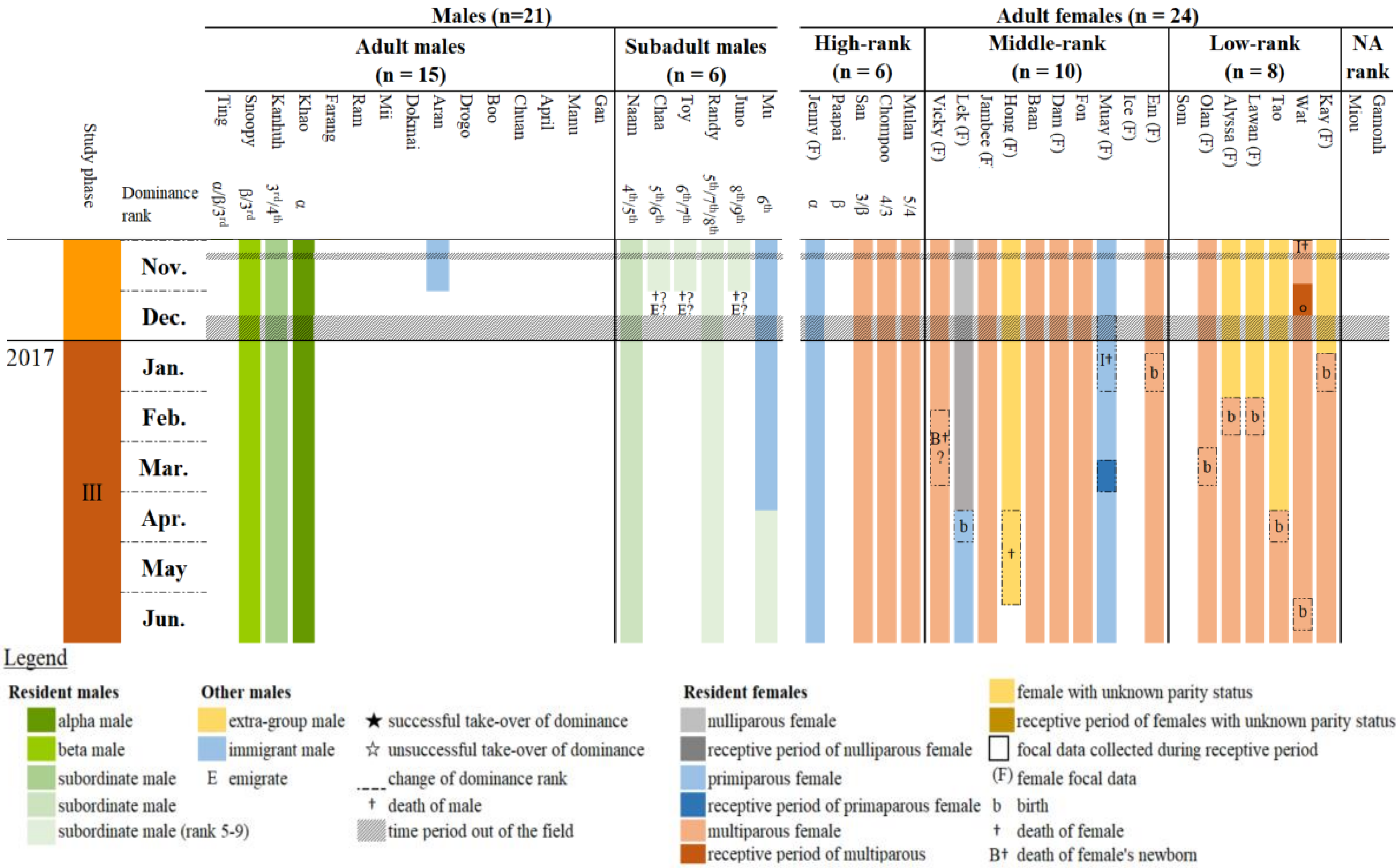


Figure 3.1 Demography of CH group from September 2015 to June 2017 at Khao Yai National Park, Thailand. Continued.

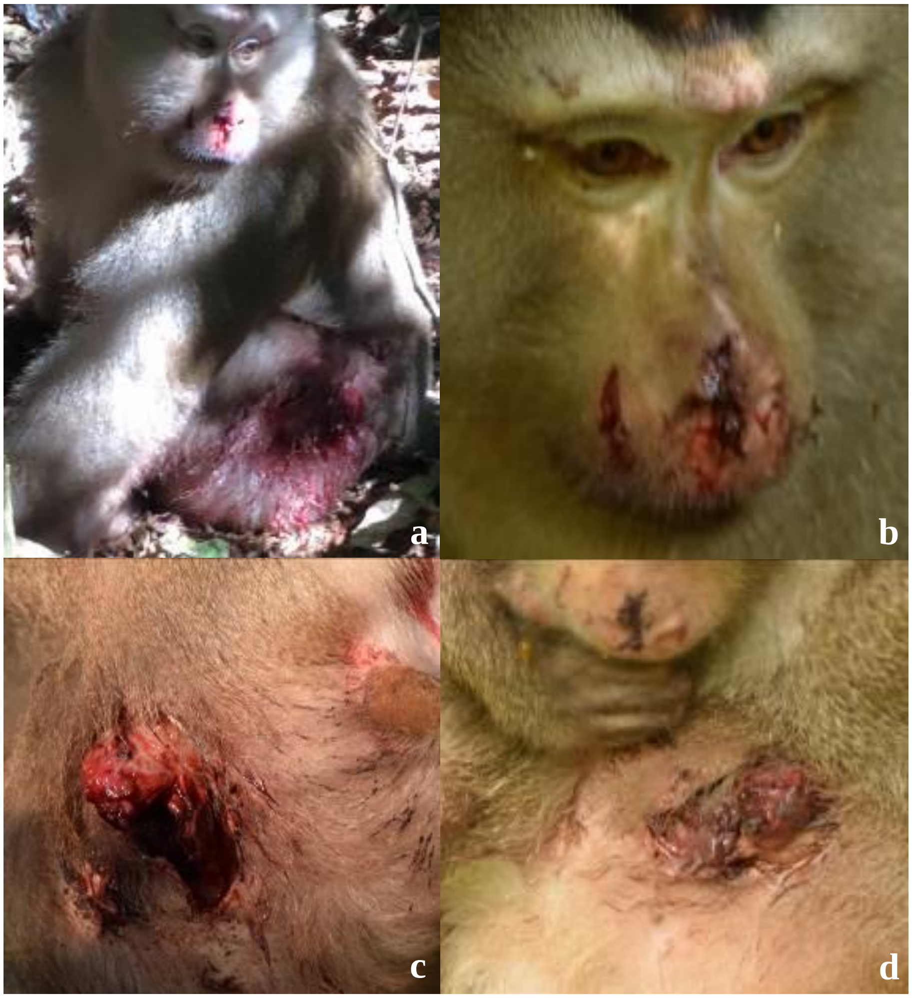


Figure 3.2 Farang’s injuries on his face (2a, 2b) and left thigh with muscle’s tissue exposed and partially cut (2c), as a result of a fight with the resident males on December 21, 2015. The same injuries on Farang’s left thigh taken 2 days after the fight (2d).

Figure 3.3 Ting’s back injury as a result of a fight with Farang on December 21, 2015. The injury is being cleaned by Mulan, an adult female, on December 23, 2015.

Figure 3.4 Ting’s injuries (4a: forehead, 4b: face, 4c: throat) as a result of a fight with Khao on April 4, 2016.

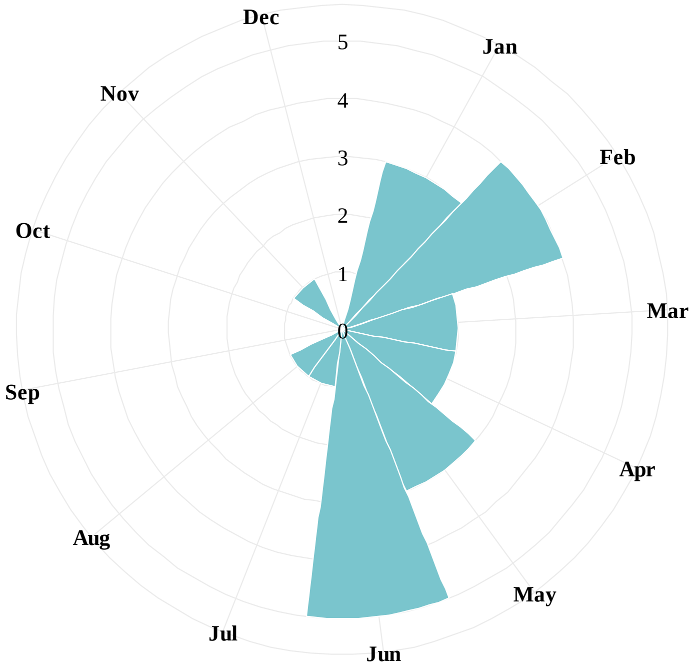


Figure 3.5 Monthly distribution of births over a one-year period in one group (CH) of wild northern pig-tailed macaques at Khao Yai National Park, Thailand (based on 22 births recorded from Jun. 2015-May 2017).

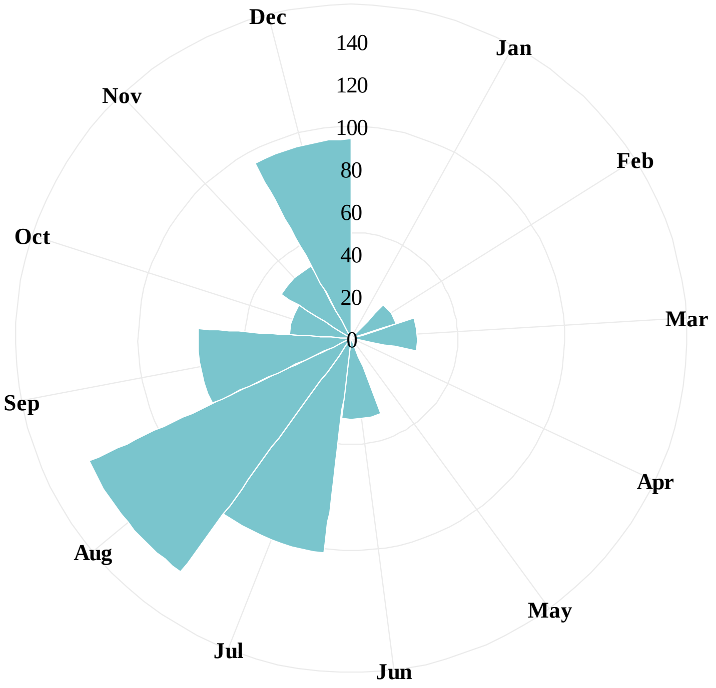


Figure 3.6 Monthly distribution of matings (copulations and ejaculatory copulations) from adults over a one-year period in one group (CH) of wild northern pig-tailed macaques at Khao Yai National Park, Thailand (based on 563 copulations recorded from Nov. 2015-Oct. 2016).

CHAPTER 4

TESTING THE PRIORITY-OF-ACCESS MODEL IN A MODERATELY SEASONNALLY BREEDING PRIMATE SPECIES

4.A. Introduction

In multimale group-living primates, males compete with other males for access to females to copulate with and at the same time prevent female promiscuity (Dixson & Anderson, 2002). Male dominance rank is often a direct reflection of males' competitive ability, with comparative studies suggesting a positive correlation between male rank and reproductive success (Alberts, 2012; Cowlishaw & Dunbar, 1991; Dixson, 2012; Dubuc, Ruiz-Lambides, & Widdig, 2014; Majolo et al., 2012; Soltis et al., 2001; Sukmak et al., 2014; Surbeck et al., 2017; van Noordwijk & van Schaik, 2004), with a reproductive advantage for the top-ranking alpha male (e.g., savanna baboons, *Papio cynocephalus,* Alberts et al., 2006; Assamese macaques, *Macaca assamensis*, Sukmak et al. 2014; bonobos, *Pan paniscus*, Surbeck et al., 2017; mandrills, *Mandrillus sphinx,* Setchell et al., 2005a). However, empirical studies also show that the strength of the relationship between male dominance rank and male reproductive success varies and can be weak, or even absent in some species (e.g., Kutsukake & Nunn, 2006; van Noordwijk & van Schaik, 2004). The causes for this variation and circumstances under which alpha males are unable to achieve high reproductive success remain poorly understood, highlighting the need for empirical studies investigating proximate factors that may explain variation in the distribution of male paternity among group-living primates (Dubuc et al., 2011).

One main factor that is believed to affect dominant males' reproductive success is the degree of female reproductive synchrony (female synchrony), which simply refers to the number of simultaneously sexually receptive females in a group (Paul, 2002; Setchell, 2008; van Noordwijk & van Schaik, 2004; van Schaik et al., 2004). Indeed, female anthropoids are known to engage in sexual activity beyond their five-day fertile period through displays of sexual behaviors (Dixson, 2012). When more than one female is simultaneously receptive, it becomes increasingly difficult even for the top-ranking male to monopolize all receptive females during their fertile periods, who may then also copulate with lower-ranking males (Cowlishaw & Dunbar, 1991). The degree of female synchrony depends on the number of females in the group, the females' spatial distribution, the length of females' fertile periods, and the species' degree of breeding seasonality (Kutsukake & Nunn, 2006; Ostner et al., 2008; Paul, 1997, 2002, 2004; Setchell, 2008; van Noordwijk & van Schaik, 2004; van Schaik et al., 2004).

In primates, the Priority-of-Access model (PoA model) (Altmann, 1962) is usually used to predict the effect of female synchrony on the relationship between male dominance rank and reproductive success (see Kutsukake & Nunn, 2006). The model makes explicit predictions for the expected reproductive success of each male based on his position in the male dominance hierarchy and the extent of female synchrony (Altmann, 1962). The model assumes that one male can only successfully monopolize access to a single receptive female at a time and that one copulation directly translates into one fertilization (Altmann, 1962). The model predicts that the highest-ranking males will have priority of access to copulate with and to fertilize a female over the lower-ranking males. When a single female is receptive, the model assigns all copulations/fertilizations to the alpha male; when two females are simultaneously receptive, the model assigns half of the copulations/fertilizations to the alpha and half to the second highest-ranking male, the beta male; and so on. The model allots access to a receptive female on a given day only when the male dominance rank is equal or smaller than the number of simultaneously receptive females on that day. For instance, if there are three females simultaneously receptive, the model will only assign a probability of access to these receptive females to the three top-ranking males (ranks 1-3).

So far, studies which have tested the PoA model have mainly been conducted in non-seasonally breeding primates (e.g., savanna baboons, Alberts et al., 2006; Engelhardt et al., 2006; mandrills, Setchell et al., 2005a; chimpanzees, *P. troglodytes*, Boesch et al., 2006), with only a few studies on strictly and moderately seasonally breeding primates (e.g., rhesus macaques, *M. mulatta*, Dubuc et al., 2011; Assamese macaques, Sukmak et al., 2014). Studies of non-seasonal breeders tended to support the model's predictions, finding a positive correlation between the predicted and the observed male mating/reproductive success according to dominance rank position. However, these studies also showed that the predicted mating and paternity skew towards the alpha male was usually overestimated, while the share of copulations/paternity among subordinate males was underestimated. In other words, in non-seasonal breeders, the alpha male's reproductive success was not directly proportional to his rank position, even if he sired the majority of offspring in a group and season.

To date, studies testing the PoA model in moderately and strictly seasonally breeding primates have remained scarce. Moreover, the validity of most of those studies regarding the scope of the PoA model remains unclear, because most used an indirect measure of reproductive success (i.e., mating success), rather than direct measures of male paternity (reviewed in Dubuc et al., 2011). As male mating success might not directly translate into reproductive success in primates (Brauch et al., 2007; Dubuc et al., 2011; Soltis, 2004), studies using an indirect measure of reproductive success potentially overestimate access by higher-ranking males and underestimate access by lower-ranking males to receptive females. For a deeper understanding of the broad applicability of the PoA model, including for seasonally breeding species, genetic paternity testing data are indispensable to evaluate the predictions of the PoA model in relation to quantified reproductive success (Dubuc et al., 2011).

Several proximate factors have been proposed to explain the residual variation from the mating/reproductive success predicted by the PoA model: energetic constraints on males, surreptitious copulations, stability of male dominance hierarchy, male sexual coercion potential, number of within- and extra-group male competitors, and female mate choice (Alberts, 2012; Alberts et al., 2003; Bissonnette et al., 2011; Port & Kappeler, 2010; Young, Hähndel, et al., 2013). The effect of these factors are expected to accentuate the discrepancy between predictions of the PoA model and observed mating/reproductive success in primate species with high female synchrony even more (Dubuc et al., 2011).

In this chapter, I investigate how female synchrony affects the relationship between male dominance rank, mating success, and reproductive success in wild northern pig-tailed macaques (*M. leonina*) at Khao Yai National Park (KYNP), Thailand. Northern pig-tailed macaques live in large multi-male, multi-female groups with a female-biased adult sex ratio (1:5 to 1:8 males to females, III.C.1.a. General Composition of CH Group). The data of my study group suggested that KYNP northern pig-tailed macaques are moderately seasonal breeders (Chapter 3) because mating and birth peaks were found in this study (3.C.4.c. Reproductive Seasonality) and two other studies (Carlson, 2011; Choudhury, 2008) of free ranging northern pig-tailed macaques.

These observations indicate a potential for temporal overlap among receptive periods of females. The species is also characterized by considerable sexual dimorphism in body weight (male weight: 8.9±0.4 kg, *n*=2; female weight: 5.1±0.6 kg, *n*=11; Malaivijitnond et al., 2012; Smith & Jungers, 1997) and a steep male dominance hierarchy (Carlson, 2011; Chapter 3). Both of these characteristics suggest that male competition for dominance is high in driving social relationships among males in this species. In addition, in one semi-provisioned group at KYNP, male mating success was skewed towards the alpha male and positively correlated with the male's dominance rank, indicating high male competition for mates (Carlson, 2011). Thus, as expected by the PoA model, male reproductive success is expected to be highly skewed towards the alpha male in this moderately seasonally breeding species. However, to date no genetic paternity testing has been conducted to measure male reproductive success. The northern pig-tailed macaque is thus an appropriate model to examine whether the PoA model can explain the relationship between male dominance and reproductive success in a moderately seasonally breeding species.

To test the PoA model, I looked at the relationship between male dominance rank, mating access to receptive females, and male reproductive success, and assessed to what extent female synchrony affected these relationships. According to the PoA model, males have access to receptive females according to their position in the male dominance hierarchy and the number of simultaneously receptive females in the group (Altmann, 1962). To comprehensively test the PoA model, I followed a two-step approach (adapted from Dubuc et al., 2011). First, I estimated the degree of female synchrony based on females' receptive periods, and from these data, calculated the predicted success of males (mating and reproductive success) based on the PoA model. Then, I compared the predicted success to: 1) the observed mating success based on mating behaviors; and 2) the observed reproductive success based on genetic paternity analysis.

4.B. Methods

4.B.1. Study site and subject

The study was conducted in the Mo Singto area (10 km^2, José-Domínguez, Huynen, et al., 2015; Reichard et al., 2012) in KYNP, northeastern Thailand (2,168 km^2; 14°26′42″ N, 101°21′56″ E; 130 km NE of Bangkok). Three seasons characterized the climate of KYNP: 1) a rainy season from May-October; 2) a cold season from November-February; and 3) a hot season from March-April (for further details, see 2.C. Study Site). KYNP is mainly covered by seasonal tropical forest and the altitude of the park ranges between 730-890 m above sea level (Kitamura et al., 2005; Kitamura et al., 2008; Reichard et al., 2012; Smitinand, 1989).

Data were collected systematically from September 2015-June 2017 (22 months) on the wild-feeding CH group (José-Domínguez, Huynen, et al., 2015; José-Domínguez, Savini, et al., 2015). The study period was divided into three phases. During Phase I (September-October 2015), all subadult and adult individuals of the group were identified. During Phase II (November 2015-December 2016), the main behavioral and genetic data were collected. During Phase III (January-June 2017), births of infants who were conceived during Phase II were recorded and fecal samples from adult individuals and infants for genetic paternity analyses were collected during bimonthly observations (for further details, see 2.E.1. Timeline for Data Collection).

Based on their migration status, males were differentiated into three categories: 1) resident males, defined as individuals who interacted daily with other group members according to dominance rank; 2) immigrant males, defined as individuals who stayed daily in the group for at least seven days, but mostly at the vicinity of the group, and irregularly interacted with group members; and 3) extra-group males (EGMs), defined as individuals who were observed at the vicinity of the group, but were often absent and interacted at a low rate with group members (for further details, see 3.B.2.c. Male Migration Status).

Over the 22-months field period, the composition of CH group included 6-10 resident males (3-5 adults, 3-6 subadults), 0-7 immigrant males (4 adults, 3 subadults), 18-24 adult females, and an estimated 35-45 immature individuals (Figure 3.1). Overall, CH group varied between 60-75 individuals. In addition, 14 extra-group males (EGMs) (11 adults, 3 subadults) were observed in CH's vicinity throughout the study period (3.C.1.d. Extra-group Males).

Lastly, I observed 26 female receptive periods, comprising 19 female conceptive cycles (8 in 2015 and 11 in 2016) and 7 non-conceptive cycles (5 in 2015, 2 in 2016) during Study Phase II (Table 4.1, see also Figure 3.1). Twenty two infants were born from 15 females (63%) between June 2015-May 2017 (see Figure 3.1). Among those infants, 17 were live births while three were stillbirths.

4.B.2. Behavioral data collection

One to three observers (CC-B, CB, MR, NL, and/or FT) recorded behavioral data during females' receptive periods throughout Study Phase II (four to six days a week, 7 am-6 pm; for further details, see 2.E.3. Behavioral Data Collection). From Aug.-Dec. 2016, only FT collected data. Continuous focal sampling (focal sampling) (Altmann, 1974; Martin & Bateson, 2007) were collected for 14 receptive periods (5 in 2015, 9 in 2016) of 14 females (3 nulliparous, 11 parous), including 11 conceptive cycles (4 in 2015, 7 in 2016) and 3 non-conceptive cycles (1 in 2015, 2 in 2016; Table 4.1, see also Figure 3.1). Focal sampling data were collected on receptive females at one- to three-day intervals with a total of 104.2 hours in 2015 and 454.6 hours in 2016 (Table 4.1). In addition, *ad-libitum* data (Altmann, 1974; Martin & Bateson, 2007) provided information on 12 receptive periods (8 in 2015, 4 in 2016) of 10 parous females, including 9 conceptive cycles (5 in 2015, 4 in 2016) and 3 non-conceptive cycles in 2015 (Table 4.1, see also Figure 3.1).

Focal sampling data were also collected on males (four adults, one subadult) every one to three days with a total of 59.5 hours in 2015 and 42.3 hours in 2016 (Table 4.2) between Nov. 2015-Mar. 2016. From April 2016 until the end of the study, males could not be followed during the mating period as more than two females were simultaneously receptive, and only these females were observed. During focal follows, all behavioral data were recorded on an iPad mini 4 using the Animal Behavior Pro iOS App (Newton-Fisher, 2012). Using a random number generator, focal individuals were chosen randomly to achieve an unbiased, equal daily observation time for each focal animal.

During focal follows, all occurrences of sexual behavior (copulation, ejaculatory copulation; Table 4.3) and the identity of the focal individual’s partner were recorded. In addition, *ad-libitum* observations of sexual behaviors were noted throughout the day (Altmann, 1974; Martin & Bateson, 2007). *Ad-libitum* sampling was also used to record the number of receptive females on any given observation day during Study Phases I and II. A female was categorized as sexually receptive when she was seen mating (i.e., copulation, ejaculatory copulation, evidence of sperm plug) (Dixson, 2012; Dubuc et al., 2012). A period of female sexual receptivity (receptive period) was determined as a continuous period of mating activity over consecutive days, but it could include one-to-two days of an absence of copulation (Dubuc et al., 2012).

Lastly, aggressive and submissive behaviors were recorded during focal sampling and *ad libitum* sampling. Male-male and female-female agonistic behaviors were used to determine male and female dominance rank positions.

4.B.3. Male dominance hierarchy

The male dominance hierarchy was established from all dyadic interactions of aggression and submission between two males. Bidirectional agonistic behaviors, in which two individuals aggressed each other, were not included in this analysis. Only subadult males, who engaged in agonistic interactions with adult males and copulated with receptive females, were included in the male dominance hierarchy. Immigrant males and EGMs interacted rarely with the resident males, therefore they could not be included in the dominance hierarchy. The corrected, normalized David's scores was used to assess dominance rank (de Vries et al., 2006), using the package "steepness" (Leiva & de Vries, 2014) in R v. 3.5.1 statistical software package (R Development Core Team, 2018), based on a sociometric matrix of wins calculated for each dyad (for further details, see 3.B.3. Dominance Hierarchy).

I witnessed two male take-overs of the alpha male position, each by an immigrant male (see 3.C.3. Take-overs of Male Dominance). With three-to-four adult males resident in the group at any time, the first seven months (Sep. 2015-Mar. 2016) had adult male dominance rank Ting-Snoopy-Kanhuh, briefly interrupted by approximately one week of instability when Farang took over the alpha male position (male change Ting-Farang). In April 2016, the dominance rank changed (male change Ting-Khao) and re-stabilized as Khao-Snoopy-Ting-Kanhuh for the remaining 15 months (Apr. 2016-Jun. 2017). Male dominance hierarchy was divided into three categories: high-ranking males (alpha and beta males), middle-ranking males (ranks 3-4), and low-ranking males (ranks 5-9).

4.B.4. Genetic paternity analysis

4.B.4.a. Fecal sampling. Between Sep. 2015-Jun. 2017, 97 individuals were seen in CH group and at its periphery. These included 21 males (15 adult and 6 subadult males, who were considered potential fathers), 24 adult females (who were considered potential mothers), 3 subadult females (who had not yet reached sexual maturity), and at least 49 juveniles and infants. Between Nov. 2015-Jun. 2017, 252 fecal samples were collected from 18 males representing 86% of resident, immigrant, and EGM males (no fecal sample was collected from three EGMs: Aran, April, and Manu). Fecal samples were also collected from 22 adult females of CH group (92% of the resident females), and 25 juveniles and infants (maximum of 51% of the resident individuals in these age classes). All adult and subadult males, who copulated at least once with or were seen in close spatial proximity to a receptive female, were considered potential sires, including EGMs.

Of the 20 infants born during the study, fecal samples were collected from 14. While two infants died before fecal samples could be collected, four infants were still carried so closely by their mothers that even at the end of the study, no fecal sample was obtained. In addition to the sample of newborns, 11 infants/juveniles between the ages of 1-3 years (i.e., born prior to the onset of this study) were included in fecal sampling. The sample included four infants born in

2014, who were still carried and/or nursed by their mother at the beginning of the study and thus the mother could be identified behaviorally. For the three juveniles born in 2013, who already traveled independently at the onset of the study, potential mothers were identified based on social behavior through matriline interactions. Indeed, related individuals in macaques tend to occupy a similar social rank to their mother and daughters rank just below their mother (Chapais, 2004). Maternal relatives are also known to show more affiliative and coalitionary behaviors than more distantly related or unrelated individuals (Bernstein, 1972; Koyama, 1991). Matrilineal behaviors were estimated from *ad libitum* observations.

For genetic paternity analyses, intestinal epithelial cells were collected from feces by swabbing the surface of feces with a cotton Q-tip, within 10 min of defecation. The cotton swab was immediately submerged in 2 ml of lysis buffer (0.5% SDS, 100 mM EDTA pH 8.0, 100 mM Tris-HCl pH 8.0, and 10 mM NaCl) and the solution was stored at ambient temperature until DNA extraction (Hayaishi & Kawamoto, 2006). All samples were collected with gloves and implements to avoid human contamination.

4.B.4.b. DNA extraction. DNA was extracted using QIamp® DNA Stool Mini Kit (Qiagen Inc., Hilden, Germany) using the modified manufacturer’s protocol. The 2 mL tubes were centrifuged for 10 min at 15-25°C at 20,000 g. The supernatant was transferred into a 2 mL tube and 0.4 mL of Buffer ASL was added. The sample was vortexed and centrifuged for 1 min to pellet stool particles. The supernatant was transferred into a new 2 mL tube and an InhibitEX Tablet was added to the sample and immediately vortexed for 1 min or until the tablet was completely suspended. The sample was incubated for 5 min at 15-25°C (allowing the InhibitEX matrix to absorb inhibitors) and centrifuged for 3 min (to allow pellet stool particles and inhibitors to bind to the InhibitEX matrix). The supernatant was transferred into a 2 mL tube and centrifuged for 2 min, then retransferred into a new 2 mL tube and incubated at 70°C for 1 hour with 25 µl proteinase K and 600 µl Buffer AL after having been vortexed for 15 sec.

The lysate was then vortexed for 15 s with 600 µl of ethanol (96-100%) and transferred and centrifuged for 1 min into a QIAamp spin column. The tube containing the filtrate was discarded. The QIAamp spin column was transferred to a new 2 mL collection tube and 500 µl Buffer AW1 was added. The QIAamp spin column was centrifuged for 1 min and the tube containing the filtrate was discarded. The QIAamp spin column was transferred to a new 2 mL collection tube and 500 µl Buffer AW2 was added. The QIAamp spin column was centrifuged for 3 min and the tube containing the filtrate was discarded. The QIAamp spin column was transferred to a new 2 mL collection tube and centrifuged for 1 min to dry up the column. The tube containing the filtrate was discarded and the QIAamp spin column was transferred to a new 2 mL collection tube. DNA in the QIAamp spin column was incubated with 200 µl Buffer AE for 30 min at 15-25°C before centrifugation for 1 min to elute the DNA. All centrifugations were carried out at 15-25°C at 20,000 g. The extracted DNA was then used for DNA quantification, PCR amplification, and genotyping.

4.B.4.c. DNA quantification. To avoid genotyping errors induced by allelic dropout (Morin, Chambers, Boesch, & Vigilant, 2001; Navidi, Arnheim, & Waterman, 1992; Taberlet et al., 1996), I quantified the amount of DNA for each sample to estimate the appropriate number of PCR repetitions (Morin et al., 2001). DNA was quantified by Real-Time PCR performed with a

StepOnePlus™ Real-Time PCR System (Applied Biosystems, USA) following Barelli and colleagues (2013). I used primers and probe designed for the *c-myc* gene (Smith et al. 2002).

Real-Time PCRs were carried out in a 20 µl solution containing TaqMan® Fast Advanced Master Mix (Applied Biosystems), 900 nM of each primer, 250 nM probe, and 2 µl DNA template. PCR cycle conditions were: pre-incubation at 95°C for 2 s, followed by 45 cycles of 95°C for 1 s, 60°C for 20 s. A duplicate set of standards of known DNA amount were included in each analysis. This known DNA was extracted from blood cells of a northern pig-tailed macaque and quantified by spectrophotometer. The standards were diluted to 10 ng/µl, 2.5 ng/µl, 625 pg/ µl, 156 pg/ µl, 39.1/ µl pg, and 9.8 pg/ µl. All analyses were conducted on StepOne Software v2.3 (Applied Biosystems).

4.B.4.d. STR genotyping. STR genotyping was conducted on nine polymorphic human microsatellite loci: dinucleotide D15S108 and tetranucleotides D1S1656, D2S1326, D3S1768, D6S501, D8S1106, D10S1432, D13S321, and D14S306 (Table 4.4) (Babb, McIntosh, Fernandez-Duque, Di Fiore, & Schurr, 2011; Bonhomme, Blancher, & Crouau-Roy, 2005; Chambers, Reichard, Möller, Nowak, & Vigilant, 2004; Kanthaswamy et al., 2006; Liu et al., 2013; Morin, Kanthaswamy, & Smith, 1997; Smith, Kanthaswamy, Viray, & Cody, 2000). Sequences of primers were cited from GenBank database of the National Center for Biotechnology Information (NCBI) website (http://www.ncbi.nlm.nih.gov/). All forward primers were labeled by one of four fluorescent markers: 6-FAM, VIC, NED, or PET.

STR genotyping method followed Barelli and colleagues (2013). PCR amplifications were carried out in a 20 µl solution containing PCR Buffer II for AmpliTaq Gold®, 2 mM each dNTP, 25 mM $MgCl_2$, 100 mg bovin serum albumin, 20 pmol/µl each primer, 5 unit AmpliTaq Gold®

(Applied Biosystems), and 2 µl of DNA extract. PCR cycle conditions were: pre-incubation at 95°C for 5 min, followed by 50 cycles of denaturation at 95°C for 30 s, annealing at 48°C for 30 s, and extension at 72°C for 30 s, and ended with a final extension at 72°C for 10 min (Table 4.4).

All PCR products were genotyped by fragment analysis on an ABI3730XL capillary analyzer using Macrogen, Inc. (Republic of Korea). Before fragment analysis, PCR products labeled by different fluorescent colors were mixed together into three multiplex as described in Table 4.4. The standard size used was Genescan™ 600 LIZ. According to the quantity of DNA measured (Morin et al., 2001), two to seven independent PCR cycles were repeated for each locus. Fragment analysis samples were analyzed on Peak Scanner Software 1.0. CERVUS 3.0 (Kalinowski et al., 2007) was used to calculate observed and expected heterozygosity, to test deviation from Hardy–Weinberg equilibrium (HWE), and to estimate a null-allele frequency for each locus.

<u>4.B.4.e. Paternity and maternity tests.</u> For genotyped infants born during the data collection period, the number of potential sires varied from 9-15. Potential sires for infants/juveniles conceived in 2012-2014 were assumed to be males observed during this and a previous field study (pers. comm., José-Domínguez). However, for the juveniles born prior to 2014, not all potential sires were known.

I used CERVUS 3.0 (Kalinowski et al., 2007) to assign paternity. This program determines the most likely father among a pool of potential fathers based on a computer simulation, taking into account genotyping errors and presence of close relatives in a study population (Marshall et al., 1998). For the paternity simulation in CERVUS, I estimated that on average approximately

86% of the 21 observed males were sampled. In accordance with other molecular genetic paternity studies using CERVUS (Boesch et al., 2006; Okada & Tamate, 2000; Strier, Chaves, Mendes, Fagundes, & Di Fiore, 2011), 10,000 paternity simulations were generated to protect false paternity assignment and genotyping error was arbitrarily set at 1%. In CERVUS, paternities were assigned at 95% confidence (relaxed confidence) and at 99% confidence (strict confidence, Kalinowski et al., 2007).

In addition to paternity assigned through likelihood, I also looked at the number of allelic mismatches between an offspring's genotype and potential sires' genotypes. If all potential fathers and enough markers are tested, all males, except the father, were excluded. For the juveniles born in 2013, the most likely mother was confirmed through CERVUS before paternity was tested to first identify maternally inherited alleles. Although potential mothers were known from behavioral observations, all genotyped adult females were considered potential mothers for the offspring born in 2014-2016 in the maternity testing.

4.B.5. Evaluating the Priority-of-Access model

I adapted methods described by Bissonnette and colleagues (2011) and Dubuc and colleagues (2011) to test the PoA model. The PoA model assumes that a male's copulation with a female is directly proportional to his reproductive success. Thus, I calculated males' predicted mating/reproductive success based on a male's rank and the number of females synchronously receptive as predicted by the PoA model (predicted mating/reproductive success). Then, I compared the predicted mating/reproductive success to: 1) the observed mating success (based on mating activity); and 2) the observed reproductive success (based on genetic paternity).

To test how well predictions of the PoA model would match with my observations of wild northern pig-tailed macaques, it is of great importance to analyze mating activity recorded during receptive periods of conceptive cycles of females and paternity assigned to the conceived offspring. These data are needed to calculate the observed male mating success and observed male reproductive success, respectively. However, for only a small fraction of seven female conceptive cycles was both the mating activity recorded during their receptive periods and paternity able to be assigned to the conceived offspring (Data Set 1).

Therefore, I decided to add two expanded data sets of larger sample sizes to test predictions of the PoA model more robustly: 1) one data set included only the mating activity recorded during receptive periods of 12 conceptive and 3 non-conceptive cycles of females, but did not include paternity assignment of the conceived offspring due to a lack of fecal samples for those offspring (Data Set 2); and 2) another data set included only paternity assigned to offspring conceived during receptive periods of 11 conceptive cycles of females, but no record of corresponding mating activity for all of the females (Data Set 3). Due to the relatively small sample size of Data Set 1 and the larger sample sizes of Data Sets 2 and 3, I decided to analyze the mating and paternity data at three levels represented by different combinations of the raw data as indicated in Data Sets 1-3 (Table 4.1). Each data set allowed me to evaluate the PoA model from a different angle:

- Data Set 1 was used to compare predicted male mating/reproductive success to observed mating and reproductive success using observations from seven conceptive cycles of females. This data set was the most comprehensive since it included mating activity recorded during focal sampling of receptive periods and paternity assigned to the conceived offspring. This data set allowed directly comparing predicted success to observed mating and reproductive success of males.

- Data Set 2 was used to compare male predicted mating success to observed mating success using observations from 12 conceptive and 3 non-conceptive cycles of females. This data set included the mating activity recorded during focal sampling of receptive periods (observed mating success) but did not include paternity data (no observed reproductive success).
- Data Set 3 was used to compare male predicted reproductive success to observed reproductive success using observations from 11 conceptive cycles of females. This data set included paternity assigned to the offspring conceived during the observation of receptive period (observed reproductive success). To calculate the predicted male reproductive success, the duration of receptive periods was determined from *ad-libitum* or focal sampling. This data set did not include mating activity (no observed mating success).

In Data Set 1 and 3, I used only behavioral observations taken during conceptive cycles of adult females to calculate predicted mating/reproductive success, as only the mating activity during conceptive cycles can translate into reproductive success (i.e., achieved sires). In Data Set 2, I used behavioral observations taken during both conceptive and non-conceptive cycles to calculate predicted mating success, because no observed reproductive success was estimated from paternity data.

4.B.5.a. Predicting males’ mating and reproductive success. I calculated predicted mating/reproductive success following assumptions of the PoA model (Altmann, 1962), which I adapted according to methods used by Chapais (1983), Dubuc and colleagues (2011), and Wroblewski (2009). According to the PoA model a male can only monopolize one female at a time on a given day and therefore he is the only male accountable for this female's mating (Altmann, 1962). Following Dubuc and colleagues (2011), the number of females simultaneously receptive on a given day equals the rank of the lowest-ranking male (and consequently the number of males) who can have access to a female. For instance, if two females are simultaneously receptive, only two males, the alpha (rank 1) and the beta male (rank 2), are presumed to have access to the receptive females. A complication in my data set was that I considered the entire receptive period rather than just the shorter fertile phase (due to a lack of female's hormonal cycle data). I avoided overestimating female synchrony by calculating an average daily number of receptive females for each receptive period (sum of the daily number of receptive females during a female's receptive period divided by the duration of the female's receptive period in days) instead of just counting the number of receptive females each day (Dubuc et al., 2011).

Thus, for each receptive period, I calculated the average of daily number of receptive females (noted DRF) rounded (up and down) to the nearest whole number. For each receptive period, all males with a dominance rank higher or equal to DRF were assigned a probability of access to these receptive females (i.e., predicted male mating and reproductive success for this female receptive period). The probability was calculated as one divided by DRF. For instance, if DRF=3 during the receptive period of a given female, then a probability of access to the female of 1/3 was assigned to the alpha (rank 1), beta (rank 2), and the third-ranking male (rank 3), and a probability of 0 to the remaining males. The final predicted mating/reproductive success for a male was equal to the sum of cumulative probabilities of access to females during all observations over females' (non-)conceptive cycle observations (Bissonnette et al., 2011; Dubuc et al., 2011).

4.B.5.b. Calculating observed mating success. For observations of each female's receptive period, the observed mating success for a male was the sum of ejaculatory copulations achieved by the male during the female's receptive period, divided by the total number of copulations achieved by all males during the female's receptive period. A male's overall mating success was the sum of the proportion of copulations of a male over all females' receptive periods. For instance, a male had 5 copulations during a female's receptive period and she engages in total in 10 copulations, then the male would have a mating success of 5/10 or 0.5. The overall mating success of a male was his summed mating success across all receptive females (e.g., 0.5 [with female 1] + 0.3 [with female 2] + 0.4 [with female 3] + 0.2 [with female 4] = 1.4 total mating success).

4.B.5.c. Estimating observed reproductive skew. Following Dubuc and colleagues (2011), three indices of reproductive skew were used to compare predicted success, observed mating success, and observed reproductive success among males according to the set of data used. First, I analyzed the relationship between dominance rank and predicted success, observed mating success, and observed reproductive success using Spearman's correlation test.

Second, I compared the proportion of the alpha male's paternity (calculated from predicted success, observed mating success, or observed reproductive success) to the remaining resident males' proportion of paternity (following van Noordwijk & van Schaik, 2004; see also Dubuc et al., 2011; Kutsukake & Nunn, 2006; Ostner et al., 2008). Following the methods of Dubuc and colleagues (2011) and van Noordwijk and van Schaik's (2004), I considered the proportion of an alpha male's paternity as: 1) high when it exceeded 50%; 2) medium when it was <50% but the highest proportion of reproductive success among males; and 3) low when it was <50% and it did not represent the highest proportion of paternity among males.

Third, I used Nonacs' binomial skew index, also called *B* index (Nonacs, 2000, 2003), to estimate a male's skew of reproductive success among males, while disregarding male dominance rank. The *B* index is a test against the null hypothesis (i.e., *B*=0) that the distribution of paternity among resident males is random. If *B* is significantly positive, the distribution of males' reproductive successes are skewed, and when it is significantly negative, males' reproductive successes are equally distributed.

4.B.6. Statistics

All statistical tests were calculated with the R v. 3.5.1 statistical software (R Development Core Team, 2018). The package "pspearman" (Savicky, 2014) for Spearman correlation test and "MASS" (Venables & Ripley, 2002) were used to investigate the influence of female synchrony on the relationship between male dominance rank, mating success, and reproductive success. The *B* index was calculated with Skew Calculator 2013 (available online: https://www.eeb.ucla.edu/Faculty/Nonacs/pi.html). All tests were two-tailed and the significance level was set to $p<0.05$ for all statistical tests.

4.C. Results

4.C.1. Female synchrony and mating partners

During Study Phases I and II (Sep. 15-Dec. 16), 26 receptive periods of 14 females were recorded (before/after rank change Ting-Khao: 14/12; Table 4.1, see also Figure 3.1), including

15 receptive periods of 13 females recorded through focal sampling (before/after rank change Ting-Khao: 6/9 receptive periods; Table 4.1). Nineteen complete female receptive periods were recorded, each lasting on average 24 days. The mean number of simultaneously receptive females on a given day of a receptive period was 2.4 females, with a maximum of 5 females (before/after rank change Ting-Khao: mean 2.7/2.4 females, min. 1/1, max. 5/5 females). Based on focal data, females accepted on average 4.1±2.4 mating partners during their receptive period (before/after rank change Ting-Khao: 2.8±1.4/5.5±2.3). Males had on average 4.5±2.6 mating partners (before/after rank change Ting-Khao: 3.4±2.7/5.1±2.5).

4.C.2. Parental assignment

4.C.2.a. Individuals' genotypes. STR genotypes were determined for 58/66 individuals sampled, including 10/13 adult males (one male was genotyped at only eight loci), 5/6 subadult males, 18/22 adult females, and 23/25 juveniles/infants. Four genotyped infants were conceived after the rank change Ting-Khao (50% of offspring conceived and born after rank change Ting-Khao). The mean number of alleles per locus ranged from 6-12, observed heterozygosity between 0.648 and 0.927, and expected heterozygosity between 0.583 and 0.854 (Table 4.5). The maximum estimated frequency of null alleles was 0.026. One locus (D3S1768) showed significant deviation from Hardy–Weinberg equilibrium (HWE) with Bonferroni correction ($p<0.001$; Table 4.5). However, I still included this locus in the paternity analyses because this locus did not show mismatches between mother-offspring dyads and its estimated null allele frequency was very low at 0.023.

4.C.2.b. Maternity assignment. For juveniles born in 2013, maternity was assigned with 99% confidence using CERVUS (Table 4.6). Mother-offspring dyads assigned by CERVUS matched behavioral observations in each case. Across nine loci, on average, the proportion of loci typed was 0.95 and the proportion of loci mistyped was 0.01.

4.C.2.c. Paternity assignment. Based on CERVUS, paternity for 16 offspring was assigned with 99% confidence (70% of total paternity tests; Table 4.6). For the seven remaining offspring (48%), paternity assignment remained below 95% confidence and paternity exclusion revealed at least two locus mismatches for all genotyped males. Thus, resident males were excluded as sires of these infants/juveniles. Based on parsimony, paternity of these seven offspring was assigned to unidentified EGMs. Juvenile Sinan and infant Lao were genotyped at seven and eight loci, respectively, instead of nine, but no paternity could be assigned. Across nine loci, on average, the proportion of loci typed was 0.95 and the proportion of loci mistyped was 0.01. For offspring genotyped and born during the field period, the number of potential sires was estimated between 9 and 15 (Table 4.6).

4.C.2.d. Resident males' paternity. Resident males accounted for 52% of paternity in CH group (*n*=12; Table 4.6, Figure 4.1). At the time of likely conception, the alpha-male sired 33% of the offspring (*n*=8), followed by the third-ranking male with 9% (*n*=2). The beta male and the fourth-ranking male each sired 4% of the offspring tested (*n*=1).

Before the rank change Ting-Khao, resident males sired 63% of the offspring (*n*=19). The alpha male Ting sired 42% of the offspring (*n*=8), the beta male Snoopy sired 5% (*n*=1), the third-ranking male Kanhuh sired 11% (*n*=2), and the fourth-ranking subadult male Naam sired

5% of the offspring (*n*=1; Table 4.6, Figure 4.1). After the rank change Ting-Khao, none of the resident males sired an offspring, but only four out of eight offspring conceived after the rank change were available for paternity analysis, which were assigned to EGMs (100% of paternity).

4.C.2.e. EGMs' paternity. Overall, EGMs sired 48% of the offspring (*n*=11; Table 4.6, Figure 4.1). In four cases, EGM paternity was confirmed, while seven cases were inferred because resident males could be excluded as a father. Before his take-over, then-EGM Farang sired 9% of the offspring (*n*=2), while EGMs Drogo and Khao each sired 4% of the offspring (*n*=1 each). Offspring sired by Farang and Khao, who both reached the alpha male position in CH group later, were older juveniles during my study and were conceived between 2012 and 2014.

Before the rank change Ting-Khao, EGMs sired 37% of CH's offspring (*n*=7; Table 4.6, Figure 4.1). Two offspring were sired by Farang, one by Khao, and the four remaining offspring were inferred sires by unidentified EGMs. The four offspring born after the rank change Ting-Khao were sired only by EGMs: Drogo and three inferred unidentified EGMs.

4.C.3. Test of the Priority-of-Access model

4.C.3.a. Data set 1: Predicted mating & reproductive successes based on female synchrony in relation to observed mating and reproductive successes (*n*=7 female conceptive cycles).

According to the PoA model, over the entire observation period, male mating & reproductive successes were predicted to be significantly skewed (*B*=0.138, *p*=0.043; Tables 4.7 and 4.8). The correlation between 'male dominance rank' and 'male mating & reproductive successes' was predicted to be significant ($r_s(7)$=-1, *p*=0.017; Tables 4.7 and IV.8, Figure 4.2). The alpha male was predicted to be the most successful sire, fathering 48.8% of the offspring (medium alpha male proportion; Tables 4.7 and 4.8).

As expected by the PoA model, observed mating success was significantly correlated with male dominance rank over the entire observation period (*rs(7)*=-0.92, *p*=0.001; Tables 4.7 and 4.8, Figure 4.2). In contrast to the PoA model, male mating success was not significantly skewed (*B*=-0.023, *p*=0.460; Tables 4.7 and 4.8). Surprisingly, the beta male controlled most of the observed copulations (28.4%; Table 4.7) but to a lower level than predicted by the PoA model. The alpha male was the second most successful (28.0% of the observed mating success; Table 4.7), followed by the fifth-ranking subadult male (15.1%). Four out of five subadult males of dominance rank four-to-eight (middle- and low-ranking males) were observed copulating with females, although the PoA model based on female synchrony predicted zero mating success for males of a lower rank than four. In addition, seven EGMs secured a large share of copulations with receptive females with 4.1% of mating success (Table 4.7).

In contrast to the predictions of the PoA model, paternity was shared only between two males, the alpha male and the fourth-ranking male (a subadult), over the entire study period. Thus, due to the high number of zero values in the matrix, no correlation was found between male dominance rank and reproductive success, and no reproductive skew analysis could be performed (Tables 4.7 and 4.8, Figure 4.2). The proportion of paternity controlled by the alpha male was lower (33.3%; Table 4.11) than expected by the PoA model (48.8%), but still within a medium alpha male proportion as predicted by the PoA model (Table 4.8). Only one other male, the fourth-ranking male, sired 16.7% of the offspring (Table 4.7). Also, for this data set, it emerged that EGMs controlled a majority of the paternity (50%; Table 4.7). Access to females by EGMs is not a factor considered in the original PoA model developed by Altmann (1962), and therefore, it is not surprising that my data does not fully agree with all predictions from the PoA model.

Dividing the observation period into before and after the rank change Ting-Khao, the PoA model predicted male mating & reproductive successes not to be skewed before and after the rank change (all *p*>0.1; Tables 4.7 and 4.8). However, the smaller sample size and lower proportion of copulations observed in each period may have affected the ability of the *B* index test to detect any significance in the skew analysis. The correlation between male dominance rank and mating & reproductive successes was predicted not to be significant before (*rs(5)*=-1, *p*=0.083; Tables 4.7 and 4.8, Figure 4.2) and after the rank change Ting-Khao (*rs(7)*=-1, p=0.333). Before the rank change Ting-Khao, the alpha male Ting was predicted to control more than half of the paternity (58.3%, high alpha male proportion; Tables 4.7 and 4.8), while after the rank change Ting-Khao, the alpha male Khao was predicted to only be as successful a sire as the beta male (41.7%, medium alpha male proportion; Tables 4.11 and 4.8).

As predicted by the PoA model, the correlation between male observed mating success and dominance rank was not significant before the rank change Ting-Khao (*rs(5)*=-0.77, *p*=0.102; Tables 4.7 and 4.8, Figure 4.2). However, dominance rank was significant after the rank change Ting-Khao (*rs(7)*=-76, *p*=0.037), in contrast to the predictions of the PoA model. Before the rank change Ting-Khao, the alpha male Ting had the highest mating success (47.4% of observed mating success; Table 4.7), but to a lower level than predicted by the PoA model. Instead of the predicted beta male Snoopy, the fourth-ranking subadult male Naam achieved the second highest mating success (24.2% of observed mating success; Table 4.7), three times higher than predicted by the PoA model. After the rank change Ting-Khao, in contrast to the expected high mating success equally shared by alpha and beta males, the beta male Snoopy was the most successfully mating male (38.3% of observed mating success; Table 4.7), followed by the fifth-ranking subadult male Naam (20.8%), who was not expected to copulate with any receptive female. The alpha male Khao achieved only 13.4% of the observed copulations, three times less than expected by the PoA model (Table 4.7).

The alpha male Ting had the highest observed reproductive success before the rank change Ting-Khao (66.7%, high alpha male proportion; Tables 4.7 and 4.8) at a higher level than predicted by the PoA model (58.3%). The fourth-ranking male Naam (a subadult) achieved the remaining paternity (33.3%; Table 4.7), four times higher than predicted by the PoA model. After the rank change Ting-Khao, in contrast to the expected medium reproductive success equally shared by the alpha and beta males, resident males sired no offspring (Table 4.7) but EGMs controlled all paternity (100%; Table 4.7).

Overall, the positive correlation between male mating success and dominance rank found in my study group fit to the predictions derived from the PoA model. Nevertheless, overall, the PoA model tended to overestimate individual male's reproductive success. The alpha male was not able successfully to control access to females as the PoA had predicted based on his rank and synchronous females alone. Subordinate males (adults and subadults) were able to copulate with receptive females and also sired offspring, and in addition a large proportion of offspring were sired by EGMs, who are not consider in the original PoA model.

4.C.3.b. Data set 2: Predicted mating success based on female synchrony in relation to observed mating success (*n*=15 female receptive periods). Based on the PoA model, over the entire observation period, male mating success was predicted to be significantly skewed (*B*=0.089, *p*=0.012; Tables 4.9 and 4.10). The association between male dominance rank and mating success was predicted to be highly significant ($r_s(7)$=-1, *p*<0.001; Tables 4.9 and 4.10, Figure

4.3). With an estimated 35.3% of paternity, the alpha male was expected to achieve the highest mating success (Tables 4.9 and 4.10).

As predicted by the PoA model, the correlation between male observed mating success and dominance rank was highly significant over the entire observation period ($r_s(7)$=-0.88, p=0.003; Tables 4.9 and 4.10, Figure 4.3). Furthermore, in contrast to the PoA model, male observed mating success was not significantly skewed (B=0.013, p=0.257; Tables 4.9 and 4.10). The beta male copulated most successfully (26.7% of observed mating success; Table 4.9), followed by the alpha male (22.5%), the fifth-ranking male (a subadult) (16.0%), and the fourth-ranking male (11.6%). However, observed mating successes were at a lower rate than predicted by the PoA model for the males with a dominance rank above four (high- and middle-ranking males of ranks 1-3), but higher than predicted by the model for the males with a rank below four (low-ranking males). For instance, the mating success of the fifth-ranking subadult male was three-times higher than predicted by the PoA model. All five subadult males of dominance rank four-to-nine were observed copulating with the females, although the PoA model based on female synchrony predicted zero mating success for males of a lower rank than five. In addition, seven EGMs copulated with receptive females, representing 3.6% of observed mating success (Table 4.9).

Dividing the observation period into before and after the rank change Ting-Khao, mating success was no longer predicted to be skewed either before or after the rank change (all p>0.1; Tables 4.9 and 4.10). The correlation between male dominance rank and mating success was predicted to be significant before ($r_s(5)$=-1, p=0.017; Tables 4.9 and 4.10, Figure 4.3) and after the change of rank ($r_s(7)$=-1, p=0.017). The alpha male was predicted to have the highest mating success (43.1%; Table 4.9) before the rank change Ting-Khao, while both the alpha male and the beta male were predicted to share the highest mating success (30.2% each; Table 4.9) after the rank change Ting-Khao.

The correlation between male observed mating success and dominance rank was significant before ($r_s(5)$=-0.89, p=0.012; Tables 4.9 and 4.10, Figure 4.3) and after the rank change Ting-Khao ($r_s(7)$=-0.78, p=0.017), as predicted by the PoA model with higher-ranking males achieving higher mating successes. Likewise, as predicted by the PoA model, male observed mating success was not significantly skewed before (B=-0.052, p=0.851; Tables 4.9 and 4.10) and after (B=-0.030, p=0.586) the rank change Ting-Khao. Before the rank change Ting-Khao, the alpha male Ting was the most successful male regarding observed mating success (35.5%; Table 4.9), followed by the beta male Snoopy (21.2%), the fourth-ranking subadult male Naam (19.0%), and the fifth-ranking subadult male Toy (14.3%). The third-ranking male Kanhuh controlled only 4.9% of observed mating success. A different pattern was observed after the rank change Ting-Khao when Khao was the alpha male. During this phase, the beta male Snoopy was the most successfully mating male (30.4% of observed mating success; Table 4.9), followed by the fifth-ranking subadult male Naam (17.2%). The alpha male Khao only occupied the third-most successful mating position with less than half of copulations of the most successfully mating male Snoopy (13.8% of observed mating success; Table 4.9). Interestingly, the third-ranking male Ting, who was the previous alpha male, remained as successful as the alpha male Khao after the rank change Ting-Khao (10.3% of observed mating success; Table 4.9).

Overall, the negative correlation between male mating success and dominance rank found in my study group, i.e. the lowest rank number (alpha male) correlating with the highest mating success, fit the predictions derived from the PoA model, despite that exactly predicted values were not replicated. The alpha male was not able to control access to females as much as the

PoA model predicted he should have been able to control access, allowing lower-ranking males (adults and subadults) to copulate with receptive females more than expected.

4.C.3.c. Data set 3: Predicted reproductive success based on female synchrony in relation to observed reproductive success (*n*=11 female conceptive cycles). According to the PoA model, over the entire observation period, male reproductive success was predicted to be significantly skewed (*B*=0.186, *p*=0.001; Tables 4.11 and 4.12). The association between male dominance rank and reproductive success was predicted to be significant ($r_s(7)$=-1, *p*=0.017; Tables 4.11 and 4.12). The alpha male was predicted to be the most successful sire, controlling 47.0 % of paternity (medium alpha male proportion; Tables 4.11 and 4.12).

In contrast to the predictions of the PoA model, male observed reproductive success was only controlled by the alpha male, the third- and fourth-ranking males, over the entire observation period (Table 4.11). The proportion of paternity controlled by the alpha male was lower than expected (36.4% observed vs. 47.0% predicted), but remained within the expectation for a medium alpha male reproductive success proportion as predicted by the PoA model (Tables 4.11 and 4.12). The third- and fourth-ranking males each sired 9.1% of the offspring (Table 4.11). Interestingly, EGMs controlled a large proportion of the paternity (45.5%; Table 4.11). Due to the large number of zero values in the matrix, no correlation could be performed between male dominance rank and reproductive success and no reproductive skew analysis was possible.

Dividing the observation period into before and after the rank change Ting-Khao, the PoA model predicted that male reproductive success was significantly skewed before (*B*=0.122, *p*=0.040; Tables 4.11 and 4.12), but not skewed after the rank change (*B*=0.032, *p*=0.100). The association between male dominance rank and reproductive success was predicted to not be significant before ($r_s(5)$=-1, *p*=0.083; Tables 4.11 and 4.12) and after the rank change Ting-Khao ($r_s(7)$=-1, *p*=0.333). Before the rank change Ting-Khao, the alpha male Ting was predicted to control half of the paternity (50.0%, high alpha male proportion; Table 4.11), while after the rank change Ting-Khao, the alpha male Khao was predicted to be as successful sire as the beta male Snoopy at 41.7% of paternity (medium alpha male proportion).

The alpha male Ting had the highest observed reproductive success before the rank change Ting-Khao (57.1%, high alpha male proportion; Tables 4.11 and 4.12), which exceeded the proportion predicted by the PoA model. The only other resident males who sired an offspring was the fourth-ranking male Naam (14.3% of offspring; Table 4.11). After the rank change Ting-Khao, when Khao was alpha male, and in contrast to the expected medium reproductive success equally shared among alpha and beta males, resident males failed to sire offspring (Tables 4.11 and 4.12), who were all attributed to EGMs (100%; Table 4.11).

Overall, male reproductive success in my study group did not exactly fit to the predictions derived from the PoA model. The model overestimated the ability of the alpha male to control access to females and underestimated the ability of subordinate males (adults and subadults) to sire offspring. In addition, the PoA model does not consider EGMs, who sired a large number of offspring.

4.D. Discussion

In my study, I tested whether the original PoA model, as developed in the 1960s, can still be considered a reliable predictor for relationships between male dominance rank, mating success, and reproductive success in multi-male primate groups (Alberts et al., 2006; Rodriguez-

Llanes, Verbeke, & Finlayson, 2009; Wroblewski et al., 2009). My results confirmed predictions of the PoA model in that it correctly predicted a significant relationship between mating success and dominance rank among resident males. However, male mating skew and the proportion of paternity controlled by the high-ranking males were lower than predicted by the PoA model during the entire study period, as well as when the relationship was investigated in the divided data set of before and after the rank change Ting-Khao. Variation of male mating and reproductive success were observed before and after a change of alpha male. In particular, great variation of observed mating and reproductive success were found between the two alpha males, despite similar proportion predicted by the PoA model. Further, this is the first study to report mating and successful paternity by EGMs in a non-seasonally breeding species with a year-round male group structure. Therefore, I suggest that proximate factors often not considered when applying the PoA model to primate populations should be considered when explaining the distribution of matings and paternity in species similar to the moderately seasonally breeding group of northern pig-tailed macaques observed in this study, but perhaps even more widely across the primate order.

In accordance with other studies (e.g., baboons, Alberts et al., 2006; chimpanzees, Boesch et al., 2006; Wroblewski et al., 2009; macaques, Engelhardt et al., 2006; Sukmak et al., 2014), the alpha male sired more offspring (36.4%) than other resident males. My data confirm that the top-ranking position is attractive for males to achieve as it comes with the prospect of priority of access to receptive females. However, in the three types of data set tested in this study, the alpha male's observed reproductive success was much lower than expected by the PoA model. The model may have overestimated the ability of the alpha male successfully to mate-guard receptive females. Indeed, as suggested in other primates (e.g., chimpanzees, Boesch et al., 2006; baboons, Alberts et al., 2006; macaques, Engelhardt et al., 2006), mate-guarding is energy-limited and time consuming. Because the male needs to follow closely the receptive females and fend off any approach of contestants, his feeding time might therefore be reduced, increasing the cost associated with mate-guarding (Alberts et al., 2006; Matsubara, 2003). Such constraints may also depend on the male's experience, as inexperienced males may have more difficulties to perform such multitasking behavior (Alberts et al., 2006). The energy/experience constraints associated with mate-guarding may also increase the difficulty in preventing surreptitious copulations by lower-ranking males, as reported in other primates (e.g., baboons, Alberts et al., 2006, rhesus macaques, Berard et al., 1994). In this study, the mating success of the middle- and lower-ranking males, including the subadult males, was much higher than expected by the PoA model. The third- and fourth-ranking males, including a subadult, were able to sire one offspring each, even though they were seen mating with receptive females at a lower rate. These results indicate that receptive females were not mate-guarded all the time by the alpha male, which allowed lower-ranking males and females to copulate successfully.

A contrasting pattern in the distribution of copulations of this study (CH group) was found in another group of northern pig-tailed macaques at KYNP (HQ group, Carlson, 2011). Based on a 15-month study period in HQ group, male dominance rank was correlated with mating success, with the alpha male successfully monopolizing 56% of observed matings (Carlson, 2011). In CH group, the alpha male was only capable of monopolizing 22.5% of observed matings (this study). The difference may be explained by: 1) a difference of female synchrony, female mate choice, and alpha male's personality between HQ and CH group; 2) higher food availability to HQ group; or 3) male dominance rank instability in CH group.

In HQ group, female synchrony as calculated in my study was not available. Only the monthly numbers of receptive females were available, which does not reveal exactly whether females were simultaneously receptive in each month. Still, by looking at the number of receptive females per month, it is possible to estimate whether receptive females were likely to overlap. One receptive female per month was observed over a six-month period in HQ group vs. a three-month period in CH group, and 4-5 receptive females per month were observed over a one-month period in HQ group vs. a three-month period in CH group. The probability of having simultaneously receptive females in HQ group over a five-month period was therefore much lower than in CH group. Consequently, it was easier to maintain control of reproduction for the alpha male in HQ group because for a long period, only a single receptive female had to be guarded. In addition, because of the higher female synchrony in CH group, there was perhaps more room for female mate choice because receptive females were probably not always mate-guarded by the alpha male. Indeed, females were observed copulating with other males, which decreased the proportion of copulations controlled by the alpha male in CH group (this study). A difference of alpha male’s personality between CH and HQ group could also affect the ability of subadult males to access receptive females. If the alpha male is not overtly aggressive when males attempt to access females, these males may achieve copulations with females, perhaps even further encouraged by female mate choice. Thus, an alpha male may be able to solicit subordinate behavior in direct male-male confrontations but may fail to enforce his dominance status when he would need to guard receptive females. By comparing the two studies (this study, Carlson, 2011), it seems to be that female synchrony and with it, female mate choice and male personality, may play a role in how tightly male rank corresponds to reproductive success.

Another factor explaining the difference of mating distribution between CH (this study) and HQ group (Carlson, 2011) may be the difference of available food between both groups. HQ group was semi-provisioned, while CH group was unprovisioned. Higher food availability is known to affect reproductive seasonality and subsequently the average number of simultaneously receptive females (Gesquiere, Altmann, Archie, & Alberts, 2018; Strum & Western, 1982). Females of HQ group may have been able to reproduce year-round, consequently decreasing female synchrony and allowing the alpha male to better control females' sexual activity compared to CH group, which was more likely affected by seasonal variation in food availability. However, HQ group was studied in 2007-2008; since then regulations have been enacted to decrease provisioning of HQ group by tourists in the national park. Since this change, it remains unclear if HQ group relies as much on natural food as CH group.

Lastly, the instability of the dominance rank in CH group may have contributed to the poor mating success of the new alpha male Khao. CH group's females may have been reluctant to accept the new alpha male, may have more often avoided him, and may have preferred mating with other resident males, such as the lower-ranking subadult male Naam. It is not known for how long female northern pig-tailed macaques may be hesitant to fully accept a new alpha male, but females in multi-male primate groups are often not immediately willing to accept new dominant males (Fedigan, 1976; Setchell, Knapp, & Wickings, 2006; Smuts, 1985; Strum, 1982). Therefore, alpha male change can be equated with social instability. The transition to the period of social stability may occur when there is a shift of mating activity to a majority of copulations with the alpha male. This shift may indicate that the alpha male is accepted as dominant male by the females. In HQ group, the dominance rank was stable (Carlson, 2011) and the alpha male controlled most copulations. In CH group (this study), before the rank change

Ting-Khao, there was a close fit between the predicted and observed mating success of the alpha male Ting, while after the rank change Ting-Khao, there was a large discrepancy between the predicted and observed mating success of the new alpha male Khao in both Data Set 1 and 2. In stable groups with prime alpha males, the PoA model may fit better than in groups with social change or social instability.

The medium concentration of paternity by the alpha male (36.4%) observed in my study group defined as moderately seasonal breeders (see Chapter 3) contrasts with the high proportion of paternity by the alpha male (over 60%) usually found in other moderately seasonally breeding groups (e.g., long-tailed macaques, *M. fascicularis*; lion-tailed macaques, *M. silenus*; savanna baboons; hanuman langurs, *Semnopithecus entellus*; reviewed in van Noordwijk & van Schaik, 2004; crested macaques, *M. nigra*, Engelhardt et al., 2017). So far, such smaller proportions of paternity have only been recorded in seasonally breeding species (e.g., 0-38%, Barbary macaques, *Macaca sylvanus*, reviewed by Bissonnette et al., 2011; 43%, toque macaques, *M. sinica*, Keane, Dittus, & Melnick, 1997; 33%, Japanese macaques, *M. fuscata*, Soltis et al., 2001). In Barbary macaques, male-male coalitions and female mate choice (preference for prime males) were the main tactics leading to a lower mating skew in the study group (Bissonnette et al., 2011). Indeed, lower-ranking males may form coalitions and harass the top-ranking males, which in turn may lose control over access to receptive females and allow lower-ranking males to copulate with the females (Bissonnette et al., 2011). Such behaviors were not observed in my study group and seems unlikely to be a factor affecting the distribution of mating and reproductive success in northern pig-tailed macaques. In Japanese macaques, short, surreptitious copulations by lower-ranking males out of sight of higher-ranking males and female mate choice (preference to copulate with different males) decreased the reproductive skew towards the alpha male, and non-troop males (members of another group) sired one-third of the offspring (Soltis et al., 2001). In the seasonal breeding rhesus macaques, the effect of dominance rank on the mating skew was also reduced because males are queuing for dominance and dominant males may not be the strongest or most attractive males (Dubuc et al., 2011). Altogether, these observations strongly suggest that the difference between the predicted success (based on female synchrony and dominance rank) and observed reproductive success in my study population may be explained by other proximate factors, such as female mate choice and alternative male reproductive tactics (e.g., male coalition, surreptitious copulation).

The presence of a seemingly large number of EGMs who were interacting with CH group in this study may be one of the most important factors that partially explains the lower than predicted ability of the high-ranking males to control access to females according to the PoA model. During the mating peaks, at least seven EGMs (up to four males at a time) were observed at the periphery of the group. Further, at least four EGMs sired nearly half of all offspring (45.5%), which was an unexpectedly high proportion of offspring in CH group. To my knowledge, this is the first study to report mating and successful paternity by EGMs in a non-seasonally breeding species with a year-round male group structure. Surprisingly, EGMs' copulations have not been reported in previous studies of wild northern pig-tailed macaques (Carlson, 2011; Choudhury, 2008; Feeroz, 2003) or wild southern pig-tailed macaques (Caldecott, 1986; Oi, 1996). Several factors may explain this absence of observation. The difficult habitat conditions (i.e., low visibility in the forest) may decrease the ability of the observer to sight such copulations. Other aspects may be that the EGMs of my study may have been already semi-habituated to observers due to the long-lasting field studies conducted on northern pig-tailed macaques around the headquarters at KYNP. In general, it is possible that even lone males in the larger headquarters area are semi-habituated due to high tourism activity.

However, observations of EGMs who copulated with receptive females have been reported in a substantial number of primates, especially in seasonally breeding species (e.g., blue monkeys, *Cercopithecus mitis stuhlmanni,* Tsingalia & Rowell, 1984; patas monkeys, *Erythrocebus patas,* Chism & Rowell, 1986; Harding & Olson, 1986; rhesus macaques, Berard, 1999; Berard et al., 1994; Japanese macaque, Huffman, 1991; Sprague, 1991a; Takahata, Suzuki, Okayasu, & Hill, 1994). Among them, extra-group mating with successful paternity have been reported in rhesus macaques (36% of sired offspring, Berard et al., 1994; 24%, Widdig et al., 2004), Japanese macaques (56%, Hayakawa 2008; 61%, Inoue & Takenaka, 2008; 33%, Soltis et al., 2001; 29%, Shotake & Nozawa, 1974), toque macaques (one-male group: 26%, multi-male group: 11%, Keane et al., 1997), chimpanzees (7%, Vigilant, Hofreiter, Siedel, & Boesch, 2001), patas monkeys (one group male: 20%, multi-male group: 50%, Ohsawa, Inoue, & Takenaka, 1993), Verreaux’s sifakas (*Propithecus verreauxi*, 42%, Lawler, 2007), and Hanuman langurs (21%, Launhardt, Borries, Hardt, Epplen, & Winkler, 2001). Such results and my result follow the prediction of van Noordwijk & van Schaik, 2004 that EGMs are more likely to access receptive females in seasonally breeding populations (strictly and moderately). Indeed, in these populations, female synchrony is more likely to be higher than in non-seasonally breeding species (Kutsukake & Nunn, 2006; Paul, 1997, 2004). High-ranking males are therefore less likely to be capable of controlling access to receptive females to the same degree as high-ranking males in non-seasonally breeding species.

Despite confirmed paternity by EGMs, copulations between EGMs and receptive females were observed at very low rates compared to resident males. Curiously, no female who conceived with an identified EGM was also observed mating with the sire. In Japanese macaques (Soltis et al., 2001), limited observation of matings with extra-group sires was also reported, even though offspring were sired by EGMs. Observing all mating of receptive females with EGMs is difficult because it is almost impossible to follow a receptive female everywhere she goes and to record all copulations in which she engages. In addition, EGMs are principally following receptive females at the edge of the group, up in the trees and/or in dense vegetation. Under those conditions, following and recording mating behavior is difficult and thus some copulations may have been missed. Finally, as reported by Soltis and colleagues (1997) in Japanese macaques, I suspect that mating with these sires occurred in secret and/or at night because a few times, sperm plugs on females were observed at dawn (i.e., as soon as there was enough light to see the individuals) in the study group. However, it is important to note that not all EGMs could be identified, thus some EGM sires may not have been identified during the paternity analysis due to a lack of their DNA samples.

The presence of EGMs reproducing successfully in northern pig-tailed macaques indicates thus that: 1) the social group is not equivalent to the reproductive unit; and 2) paternity cannot be solely attributed to resident males of bisexual groups. Such results have also been confirmed in other primates (e.g., Henzi & Lawes, 1988; Keane et al., 1997; Soltis et al., 2001) and non-primate species (e.g., great reed warbler, *Acrocephalus arundinaceus,* Birkhead & Kappeler, 2003; Hasselquist, Bensch, & von Schantz, 1996; Lubjuhn, Strohbach, Brun, Gerken, & Epplen, 1999). The body of evidence strongly suggests that promiscuous mating by EGMs cannot be considered insignificant observations anymore (Henzi & Lawes, 1988). EGMs' reproductive strategies need to be included in the typical male reproductive strategies of at least northern pig-tailed macaques, and probably more widely also in other primate species, even if studies only focus on observations of the resident males of the species' social group (Henzi & Lawes, 1988). Further multi-group studies focusing on male reproductive tactics in EGMs, their patterns of migration, and their social status throughout the year in relation to ecological and demographic factors are much needed.

Despite the ability of middle- and low-ranking males and EGMs to access receptive females, the distribution of observed mating success among males still does not explain the distribution of paternity observed in the study group. For instance, all the nine resident males of CH group copulated with receptive females but only four resident males sired offspring, and EGMs, who had a low mating success, sired almost 50% of offspring. As in rhesus macaques (Dubuc et al., 2011), mating success, but not reproductive success, was significantly correlated with dominance rank. Thus, all copulations do not equally lead to conceptions. A large proportion of copulations occurs outside of the female's fertile period, and therefore decreasing the likelihood of conception (Martin, 1992; Strier, 1994). In my study, I was lacking female hormonal cycle data, thus the window of fertility was indistinct, leading to less clear results between copulations and conceptions. Furthermore, depending on the ability of the male's to detect females' fertile periods using cues from females' sex skin swelling or other cues (data unavailable for this species), a male may concentrate his mating effort to the female's fertile period instead of the entire female's receptive period. Further studies including the hormonal cycle and sex skin swelling data for females are thus needed to determine to which degree males are able to detect the female's fertile period and which copulations lead to conceptions.

Factors at the post-copulatory level could also explain the mismatch between mating and paternity distribution observed in my study group. As the dominant males could not monopolize access to the females, female promiscuous mating could lead to sperm competition within the female reproductive tract (Birkhead & Hunter, 1990). Compared to birds or insects (Birkhead & Kappeler, 2003; Birkhead & Møller, 1998), factors affecting success in sperm competition remain poorly documented in primates (Setchell & Kappeler, 2003). However, there is some evidence that sperm quantity and quality may result in variation of primate male fertilization success (e.g., chimpanzees, Harcourt et al., 1981; muriquis, *Brachyteles arachnoides*, Strier, 1999; savanna baboons and rhesus macaques, Bercovitch, 1992). For instance, the beta male Snoopy in my study group may have produced sperm in lower quantity and/or quality than other males, which could explain his fairly high mating success but failure in conceptions. Once sperm from different males have been deposited inside the female reproductive tract, sperm may also be affected by cryptic female choice which can bias male paternity success (see Setchell & Kappeler, 2003). The mechanisms of cryptic female choice are still poorly understood, but factors such as the length and complexity of the vagina, uterus, and oviduct, and the composition of female secretions, are believed to play important roles (Birkhead & Kappeler, 2003; Dixson, 2012; Setchell & Kappeler, 2003). Any of those post-copulatory mechanisms could potentially explain some of the discrepancy between observed mating and reproductive success in my study group. Therefore, this study reinforces previous findings that mating success cannot be used solely as a predictor of reproductive success, and genetic paternity data are required to measure reproductive success (Brauch et al., 2007; Dubuc et al., 2011; Soltis, 2004).

Despite its novel and exciting results, my study also suffered from some limitations. First, I used female’s mating activity to determine female’s receptive period rather than hormonal data to determine female’s fertile phase. As dominant males may time their mating effort to the fertile phase of the female if they can identify it (Engelhardt et al., 2006; Heistermann et al., 2008; Higham et al., 2012), considering the entire receptive period instead of just the shorter fertile period may have led to an overestimation of predicted and observed mating success in middle- and low-ranking males (Dubuc et al., 2011). However, a study on rhesus macaques comparing both methods (receptive period vs. fertile phase) showed only minor differences in estimating male predicted and observed mating successes (Dubuc et al., 2011). Second, the interpretation of the genetic paternity data may be used with some caution. The results are from across five birth cohorts from one social group, and DNA from all offspring born during these five birth cohorts could not be collected. Thus, the paternity measured in this study is not directly equivalent to the overall paternity of all the offspring born between the years 2013-2017. The proportion of offspring sired by EGMs per year might be lower/higher. However, it does not undermine the fact that the alpha male controlled most of the paternity and EGMs sired (a not insignificant number of) offspring in CH group.

In conclusion, my results by and large support the predictions of the PoA model. A significant relationship between mating success and dominance rank was found among resident males in northern pig-tailed macaques. However, the distribution of male reproductive success indicated that: 1) the alpha male controls a lower proportion of paternity than predicted by the PoA model; and 2) EGMs, excluded from the PoA model, controlled a relatively large proportion of paternity despite a low mating success. Therefore, mating success cannot be used solely as a measure of reproductive success, confirming the need of genetic paternity data. The PoA model based on female synchrony can be used as a basic model but additional factors must be considered to describe the distribution of reproductive success, especially in moderately and strictly seasonally breeding species. An extended version of the PoA model is thus needed, widening the scope of the existing PoA model. Additional proximate factors should be included in this extended version of the PoA model, such as mate-guarding costs, surreptitious copulations by lower-ranking males and EGMs, male coalitions, and female mate choice.

Table 4.1 Types (focal and *ad libitum* sampling) and amount (hours, days) of behavioral data collected for each female in relation to the duration of their receptive period and how they were used in the data analysis (Data Set).

Study year	**Female names**	**Conceptive (C)/ Non-conceptive (NC) cycle**	**No. of focal hours**	**No. of focal days**	**Average number of focal hour/day of observation**	**Duration of receptive period (days)**	**Test of PoA model**		
							Data Set 1	*Data Set 2*	*Data Set 3*
2015	Jambee	C	20.48	13	1.58	19	X	X	X
	Muay	C	27.53	15	1.84	17	X		
	Jenny	C	19.65	15	1.31	22	X	X	X
	Ice	C	19.25	13	1.48	18	X		
	Dam	NC	17.25	10	1.73	15	X		
	Mulan	C	*Ad.-lib.*	*Ad.-lib.*	*Ad.-lib.*	27		X	
	San	C	*Ad.-lib.*	*Ad.-lib.*	*Ad.-lib.*	18		X	
	Baan	C	*Ad.-lib.*	*Ad.-lib.*	*Ad.-lib.*	21		X	
	Wat	C	*Ad.-lib.*	*Ad.-lib.*	*Ad.-lib.*	19		X	
			Total 2015: 104.2	*Avg. 2015: 13.2*	*Avg. 2015: 1.59*	*Avg. 2015: 18.2*			
2016	Dam	C	46.05	17	2.71	18	X	X	X
	Kay	C	103.4	43	2.40	47+	X	X	X
	Em	C	42.2	20	2.11	23+	X	X	X
	Lawan	C	36.35	19	1.91	43	X	X	X
	Hong	C	31.45	16	1.97	18	X		
	Alyssa	C	47.75	19	2.51	23+	X		
	Lek	NC	29.45	15	1.96	20	X		
	Vicky	NC	61.8	29	2.13	30	X		
	Olan	C	35.35	19	1.86	23	X		
	Lek	C	20.75	9	2.31	33	X	X	X
			Total 2016: 454.6	*Avg. 2015: 20.6*	*Avg. 2015: 2.19*	*Avg. 2016: 27.8*			
2015/2016			*Total 2015/16: 558.7*	*Avg. 2015/16: 18.13*	*Avg. 2015/16: 1.99*	*Avg. 2015/16: 23.9*			

+ receptive period could not be accurately estimated, the number indicates the minimum duration of the receptive period

Table 4.2 Types (focal and *ad libitum* sampling) and amount (hours, days) of behavioral data collected for each male.

Study year	**Male names**	**No. of focal hours**
2015	Ting	18.15
	Snoopy	10.45
	Kanhuh	11.15
	Farang	14.65
	Naam	5.1
	Total	*59.5*
2016	Ting	14
	Snoopy	14.3
	Kanhuh	13.95
	Total	*42.3*
2015/2016	*Total*	*101.8*

Table 4.3 Definition of sexual behaviors displayed by male and female northern pig-tailed macaques and recorded in this study.

Sexual behaviors	**Definitions**
Copulation	A series of one or more than one mount without ejaculation ending when the copulating pair is more than 10 m away from each other for more than 20 min and no ejaculation was observed (Manson, 1996; Overduin-de Vries et al., 2012; Soltis et al., 1999).
Ejaculation	Sustained deep intromission pause (or ejaculatory pause) with body rigidity and slight quivering. The male may dilate and contract repetitively his anus (adapted from Goldfoot, 1971) and may display an ejaculation face. An ejaculation was confirmed by the presence of a sperm plug around the female genital area and/or on the male's penis after the copulation (Setchell et al., 2005a; Young, Majolo, et al., 2013).
Ejaculation face	An open-mouthed expression on the male's face during ejaculation (adapted from Goldfoot et al., 1975).
Ejaculatory copulation	A series of one or more than one mount ending by one ejaculatory mount (Manson, 1996; Overduin-de Vries et al., 2012; Soltis et al., 1999).
Intromission	Penile insertion into vagina with deep and regular pelvic thrusting (adapted from Goldfoot, 1971; Overduin-de Vries et al., 2012).
Mating	A mount series with or without ejaculation (Soltis et al., 2001).
Mount	A male climbing on the female's hindquarter by placing his hands on female's hips or back and by clasping one or both of her legs with his feet, followed by intromission (adapted from Goldfoot, 1971; Manson, 1996; Overduin-de Vries et al., 2012).

Table 4.4 Summary of nine human microsatellite loci used for northern pig-tailed macaques and PCR conditions.

Locus	**Marker**	**Forward primer**	**Reverse primer**	**GenBank Accession Number**	**Repeat motif**	**Annealing temp. (°C)**	**No. of PCR cycles**	**Multiplex for fragment analysis**
D1S1656	6-FAM	GTGTTGCTCAAGGGTCAACT	GAGAAATAGAATCACTAGGGAACC	G07820	Tetra	48	50	2
D2S1326	6-FAM	AGACAGTCAAGAATAACTGCCC	CTGTGGCTCAAAAGCTGAAT	G08136	Tetra	48	50	1
D3S1768	PET	GGTTGCTGCCAAAGATTAGA	CACTGTGATTTGCTGTTGGA	G08287	Tetra	48	50	2
D6S501	PET	GCTGGAAACTGATAAGGGCT	GCCACCCTGGCTAAGTTACT	G08551	Tetra	48	50	3
D8S1106	6-FAM	TTGTTTACCCCTGCATCACT	TTCTCAGAATTGCTCATAGTGC	G09378	Tetra	48	50	1
D10S1432	PET	CAGTGGACACTAAACACAATCC	TAGATTATCTAAATGGTGGATTTCC	G08816	Tetra	48	50	1
D13S321	NED	TACCAACATGTTCATTGTAGATAGA	CATACACCTGTGGACCCATC	G08990	Tetra	48	50	3
D14S306	VIC	AAAGCTACATCCAAATTAGGTAGG	TGACAAAGAAACTAAAATGTCCC	G09055	Tetra	48	50	3
D15S108	VIC	AGGAGAGCTAGAGCTTCTAT	GTTTCAACATGAGTTTCAGA	-	Di	48	50	2

Table 4.5 Allele frequency and heterozygosity of nine human microsatellite loci used for *M. leonina*.

Locus	**No. of individuals**	**Size range (bp)**	**Heterozygosity**			**HWE**	**Null allele frequency**
			No. of alleles	*Observed*	*Expected*		
D1S1656	55	136-160	7	0.891	0.789	0.8346	-0.0678
D2S1326	55	264-300	11	0.927	0.831	0.1684	-0.0629
D3S1768	54	148-240	12	0.815	0.854	<0.001*	0.023
D6S501	54	167-207	10	0.815	0.848	0.4029	0.0109
D8S1106	55	141-165	7	0.800	0.790	0.7199	-0.0081
D10S1432	55	140-164	8	0.745	0.769	0.4038	0.0111
D13S321	54	170-195	8	0.648	0.583	0.9754	-0.0707
D14S306	55	168-199	8	0.855	0.823	0.5624	-0.0206
D15S108	55	171-183	6	0.673	0.711	0.3965	0.0264

HWE: $\chi 2$-test of Hardy–Weinberg equilibrium (*p*-value);
*Significant *p*-value with Bonferroni correction.

Table 4.6 Paternity results of 23 offspring of northern pig-tailed macaques born in CH group at Khao Yai National Park, Thailand.

Offspring	**Mother (No. of mismatches)**	**Potential fathers**				**Assigned paternity**					
						Resident males				**EGMs**	
		Primary candidate (No. of mismatches)	Secondary candidate (No. of mismatches)	No. of other candidate males [mismatch range]	No. of potential fathers genotyped/ observed (%)	Alpha male	Beta male	Third-ranking male	Fourth-ranking male	Confirmed	Inferred
Conceived in 2012											
Isinton	Em (0)$^{+}$	Ting (0)	Chaa (3)	13 [3-7]	-	**					
Onnika	Olan (0)$^{+}$	Khao (1)	Snoopy (3)	13 [4-7]	-					**	
Patma	Paapai (0)$^{+}$	Ting (0)	Snoopy (4)	13 [4-7]	-	**					
Conceived in 2013											
Chui	Chompoo (0)	Snoopy (0)	Ting (2)	13 [4-7]	-		**				
Isan	Ice (0)	Drogo (4)	Chaa (4)	13 [4-7]	-						X
Sinan	San (0)	Ram (2)	Ting (3)	13 [3-6]	-						X
Weera	Wat (1)	Snoopy (2)	Khao (5)	13 [5-8]	-						X
Conceived in 2014											
Kaia	Kay (0)	Ting (0)	Randy (2)	13 [3-7]	-	**					
Isaree	Em (0)	Farang (0)	Juno (4)	13 [4-7]	-					**	
Olivia	Olan (0)	Kanhuh (0)	Chaa (3)	13 [4-8]	-			**			
Conceived in 2015											
Boonmee	Baan (0)	Kanhuh (0)	Snoopy (3)	6 [5-6]	8/9 (89)			**			
Chailai	Chompoo (0)	Ting (0)	Randy (3)	13 [3-8]	-	**					
Flo	Fon (0)	Farang (0)	Chaa (3)	13 [5-8]	-					**	
James	Jambee (0)	Ting (0)	Naam (4)	6 [4-7]	8/9 (89)	**					
Joe	Jenny (0)	Naam (0)	Randy (4)	7 [5-8]	9/11 (82)				**		
Mai	Mulan (0)	Ting (0)	Kanhuh (3)	6 [3-8]	8/9 (89)	**					
Sapo	San (0)	Ting (0)	Snoopy (2)	6 [5-8]	8/9 (89)	**					
Wonapa	Wat (0)	Naam (4)	Chaa (5)	7 [4-7]	9/11 (82)						X
Conceived in 2016											
Dao	Dam (0)	Ting (0)	Mii (2)	7 [4-7]	9/12 (75)	**					
Total before rank change Ting-Khao (%)						**8 (42)**	**1 (5)**	**2 (11)**	**1 (5)**	**3 (16)**	**4 (21)**
						12 (63)				**7 (37)**	
Conceived in 2016											
Eve	Em (0)	Snoopy (3)	Juno (4)	11 [4-7]	12/15 (80)						X
Keng	Kay (0)	Drogo (0)	Gan (3)	11 [4-7]	12/15 (80)					**	
Lao	Lawan (1)	Gan (2)	Toy (3)	12 [3-7]	13/15 (87)						X
Leif	Lek (0)	Gan (2)	Chaa (2)	13 [3-8]	-						X
Total after rank change Ting-Khao (%)						**0 (0)**	**0 (0)**	**0 (0)**	**0 (0)**	**1 (25)**	**3 (75)**
						0 (0)				**4 (100)**	
Total before and after rank change Ting-Khao (%)						**8 (35)**	**1 (4)**	**2 (9)**	**1 (4)**	**4 (17)**	**7 (31)**
						12 (52)				**11 (48)**	

**: 99% confidence level; $^{+}$mother assigned by maternity test with 99% confidence level.

Table 4.7 Comparisons of the predictions of the PoA model (male's predicted success based on female synchrony) with male's observed mating success (proportion of copulations) and observed reproductive success (number of infants sired) from Data Set 1 before and after rank change Ting-Khao, and during the entire study period.

Male dominance rank	**Before rank change Ting-Khao**			**After rank change Ting-Khao**			**Entire study period**		
	Predicted success (%)	Mating success (%)	Reproductive success (%)	Predicted success	Mating success (%)	Reproductive success (%)	Predicted success (%)	Mating success	Reproductive success (%)
1	1.75 (58.3)	1.42 (47.4)	2 (66.7)	1.67 (41.7)	0.54 (13.4)	0 (0)	3.42 (48.8)	1.96 (28)	2 (33.3)
2	0.75 (25.0)	0.46 (15.3)	0 (0)	1.67 (41.7)	1.53 (38.3)	0 (0)	2.42 (34.5)	1.99 (28.4)	0 (0)
3	0.25 (8.3)	0 (0)	0 (0)	0.67 (16.7)	0.33 (8.3)	0 (0)	0.92 (13.1)	0.33 (4.7)	0 (0)
4	0.25 (8.3)	0.73 (24.2)	1 (33.3)	0 (0)	0.18 (4.5)	0 (0)	0.25 (3.6)	0.90 (12.9)	1 (16.7)
5	0 (0)	0.23 (7.5)	0 (0)	0 (0)	0.83 (20.8)	0 (0)	0 (0)	1.06 (15.1)	0 (0)
6	0 (0)	0 (0)	0 (0)	0 (0)	0.29 (7.3)	0 (0)	0 (0)	0.29 (4.2)	0 (0)
7	0 (0)	0.11 (3.6)	0 (0)	0 (0)	0.04 (0.9)	0 (0)	0 (0)	0.14 (2)	0 (0)
8	-	-	-	0 (0)	0.04 (0.9)	0 (0)	0 (0)	0.04 (0.5)	0 (0)
9	-	-	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
EGMs	-	0.06 (2)	0 (0)	-	0.23 (5.6)	3 (100)	-	0.29 (4.1)	3 (50)
Total	3 (100)	3 (100)	3 (100)	4 (100)	4 (100)	3 (100)	7 (100)	7 (100)	6 (100)

Table 4.8 Results of three indices of reproductive skew (relationships to dominance rank, *B* skew index, and alpha male proportion) to compare the predictions of the PoA model (male's predicted success based on female synchrony) with male's observed mating success (proportion of copulations) and observed reproductive success (number of infants sired) from Data Set 1 before and after rank change Ting-Khao, and during the entire study period.

	Before rank change Ting-Khao			**After rank change Ting-Khao**			**Entire study period**		
	Predicted success	Mating success	Reproductive success	Predicted success	Mating success	Reproductive success	Predicted success	Mating success	Reproductive success
Dominance rank	$r_s(5)$=-1, *p*=0.083	$r_s(5)$=-0.77, *p*=0.102	NA	$r_s(7)$=-1, *p*=0.333	$r_s(7)$=-0.76, *p*=0.037*	NA	$r_s(7)$=-1, *p*=0.017*	$r_s(7)$=-0.92, *p*=0.001*	NA
B index	*B*=0.012, *p*=0.378	*B*=-0.109, *p*=0.152	NA	*B*=0.032, *p*=0.100	*B*=-0.097, *p*=1	NA	*B*=0.138, *p*=0.043*	*B*=-0.023, *p*=0.460	NA
Alpha male proportion	58.3% (high)	47.4% (medium)	66.7% (high)	41.7% (medium)	13.4% (low)	0% (low)	48.8% (medium)	28.0% (low)	33.3% (low)

*: $p \leq 0.05$.

Table 4.9 Comparisons of the predictions of the PoA model (male's predicted success based on female synchrony) with male's observed mating success (proportion of copulations) from Data Set 2 before and after rank change Ting-Khao, and during the entire study period.

Male dominance rank	**Before rank change Ting-Khao**		**After rank change Ting-Khao**		**Entire study period**	
	Predicted success (%)	Mating success (%)	Predicted success (%)	Mating success (%)	Predicted success (%)	Mating success (%)
1	2.58 (43.1)	2.13 (35.5)	2.72 (30.2)	1.24 (13.8)	5.30 (35.3)	3.37 (22.5)
2	1.58 (26.4)	1.27 (21.2)	2.72 (30.2)	2.74 (30.4)	4.30 (28.7)	4.01 (26.7)
3	1.08 (18.1)	0.29 (4.9)	1.72 (19.1)	0.92 (10.3)	2.80 (18.7)	1.22 (8.1)
4	0.75 (12.5)	1.14 (19)	1.05 (11.7)	0.60 (6.7)	1.80 (12)	1.74 (11.6)
5	0 (0)	0.86 (14.3)	0.80 (8.9)	1.55 (17.2)	0.80 (5.3)	2.40 (16)
6	0 (0)	0.14 (2.3)	0 (0)	0.29 (3.2)	0 (0)	0.43 (2.9)
7	0 (0)	0.11 (1.8)	0 (0)	0.84 (9.3)	0 (0)	0.94 (6.3)
8	-	-	0 (0)	0.10 (1.1)	0 (0)	0.10 (0.7)
9	-	-	0 (0)	0.25 (2.8)	0 (0)	0.25 (1.7)
EGMs	-	0.06 (1.0)	-	0.48 (5.3)	-	0.54 (3.6)
Total	6 (100)	6 (100)	9 (100)	9 (100)	15 (100)	15 (100)

Table 4.10 Results of three indices of reproductive skew (relationships to dominance rank, *B* skew index, and alpha male proportion) to compare the predictions of the PoA model (male's predicted success based on female synchrony) with male's observed mating success (proportion of copulations) from Data Set 2 before and after rank change Ting-Khao, and during the entire study period.

	Before rank change Ting-Khao		**After rank change Ting-Khao**		**Entire study period**	
	Predicted success	Mating success	Predicted success	Mating success	Predicted success	Mating success
Dominance rank	$r_s(5)=-1$, $p=0.017$*	$r_s(5)=-0.89$, $p=0.012$*	$r_s(7)=-1$, $p=0.017$*	$r_s(7)=-0.78$, $p=0.017$*	$r_s(7)=-1$, $p<0.001$**	$r_s(7)=-0.88$, $p=0.003$*
B index	$B=0.017$, $p=0.163$	$B=-0.052$, $p=0.851$	$B=0.030$, $p=0.190$	$B=-0.030$, $p=0.586$	$B=0.089$, $p=0.012$*	$B=0.013$, $p=0.257$
Alpha male proportion	43.1% (medium)	35.5% (medium)	30.2% (medium)	13.8% (low)	35.3% (medium)	22.5% (low)

*: $p \leq 0.05$.

Table 4.11 Comparisons of the predictions of the PoA model (male's predicted success based on female synchrony) with male's observed reproductive success (number of infants sired) from Data Set 3 before and after rank change Ting-Khao, and during the entire study period.

Male dominance rank	**Before rank change Ting-Khao**		**After rank change Ting-Khao**		**Entire study period**	
	Predicted success (%)	Reproductive success (%)	Predicted success (%)	Reproductive success (%)	Predicted success (%)	Reproductive success (%)
1	3.50 (50)	4 (57.1)	1.67 (41.7)	0 (0)	5.17 (47)	4 (36.4)
2	2.50 (35.7)	0 (0)	1.67 (41.7)	0 (0)	4.17 (37.9)	0 (0)
3	0.50 (7.1)	0 (0)	0.67 (16.7)	0 (0)	1.17 (10.6)	1 (9.1)
4	0.50 (7.1)	1 (14.3)	0 (0)	0 (0)	0.50 (4.5)	1 (9.1)
5	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
6	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
7	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
8	-	-	0 (0)	0 (0)	0 (0)	0 (0)
9	-	-	0 (0)	0 (0)	0 (0)	0 (0)
EGMs	-	2 (28.6)	-	4 (100)	-	5 (45.5)
Total	7 (100)	7 (100)	4 (100)	4 (100)	11 (100)	11 (100)

Table 4.12 Results of three indices of reproductive skew (relationships to dominance rank, *B* skew index, and alpha male proportion) to compare the predictions of the PoA model (male's predicted success based on female synchrony) with male's observed reproductive success (number of infants sired) from Data Set 3 before and after rank change Ting-Khao, and during the entire study period.

	Before rank change Ting-Khao		**After rank change Ting-Khao**		**Entire study period**	
	Predicted success	Reproductive success	Predicted success	Reproductive success	Predicted success	Reproductive success
Dominance rank	$r_s(5)$=-1, p=0.083	NA	$r_s(7)$=-1, p=0.333	NA	$r_s(7)$=-1, p=0.017	NA
B index	B=0.122, p=0.040*	NA	B=0.032, p=0.100	NA	B=0.186, p=0.001*	NA
Alpha male proportion	50% (high)	57.1% (high)	41.7% (medium)	0% (low)	47.0% (medium)	36.4% (medium)

*: p ≤ 0.05.

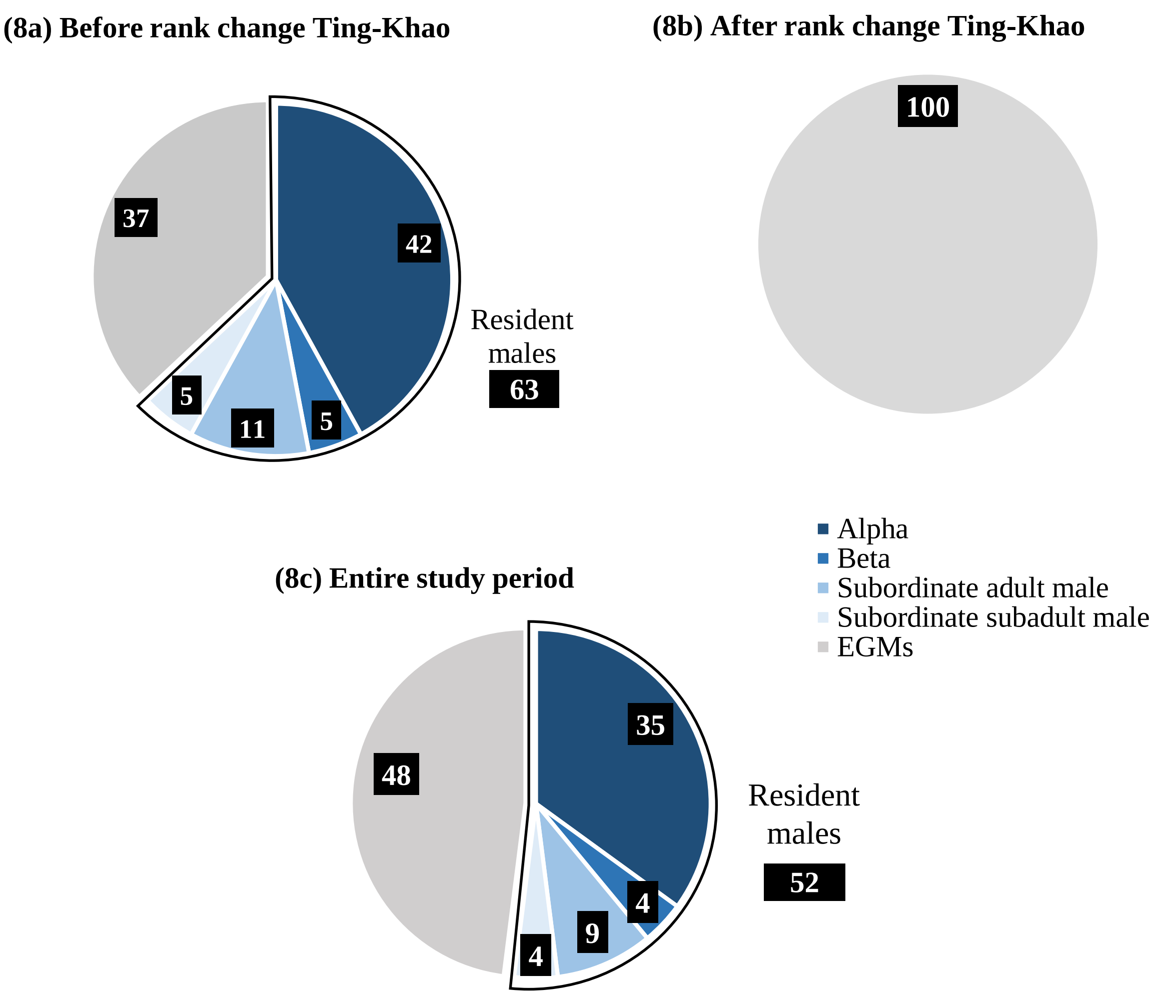
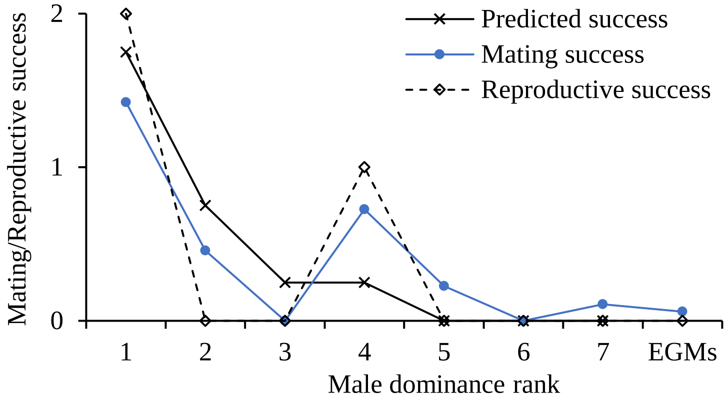
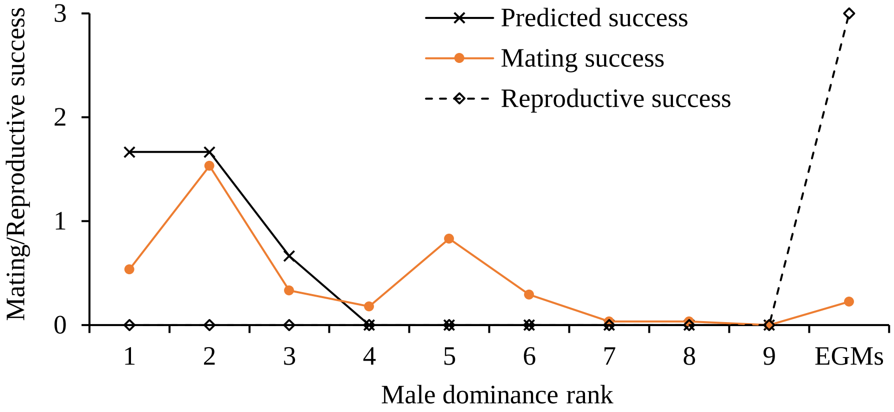


Figure 4.1 Male's shared paternity (%) of 23 offspring among resident males and EGMs of CH group before (1a) (*n*=19 infants sired) and after (1b) (*n*=4 infants sired) rank change Ting-Khao and during the entire study period (1c) at Khao Yai National Park, Thailand.

(9a) Before rank change Ting-Khao



(9b) After rank change Ting-Khao



(9c) Entire study period

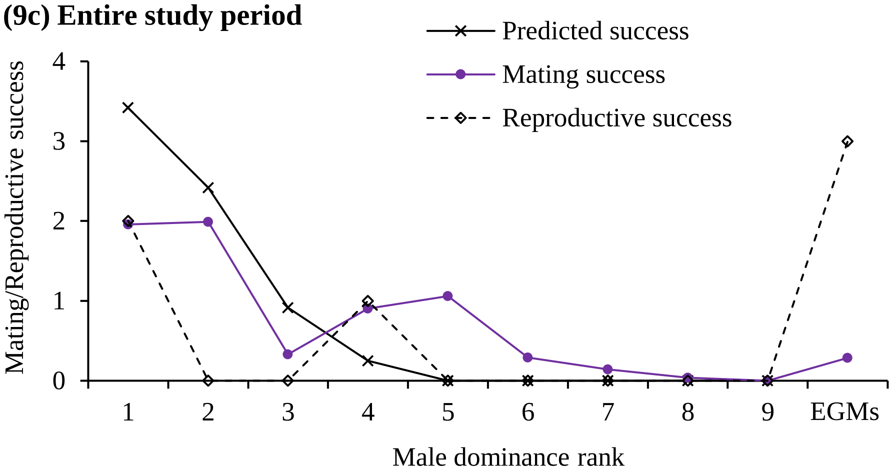
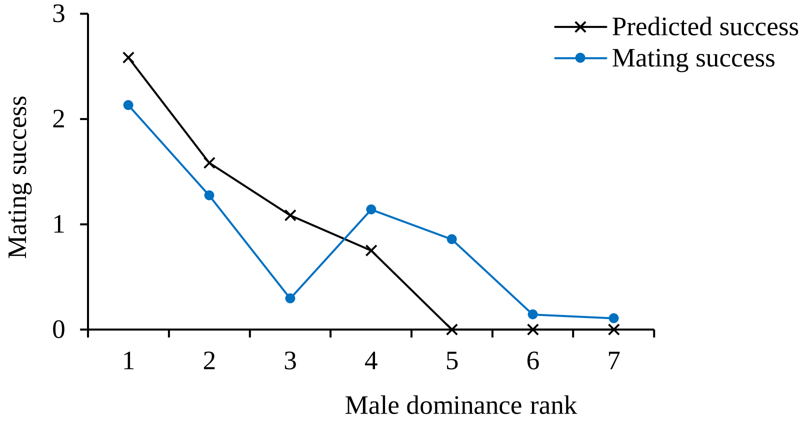
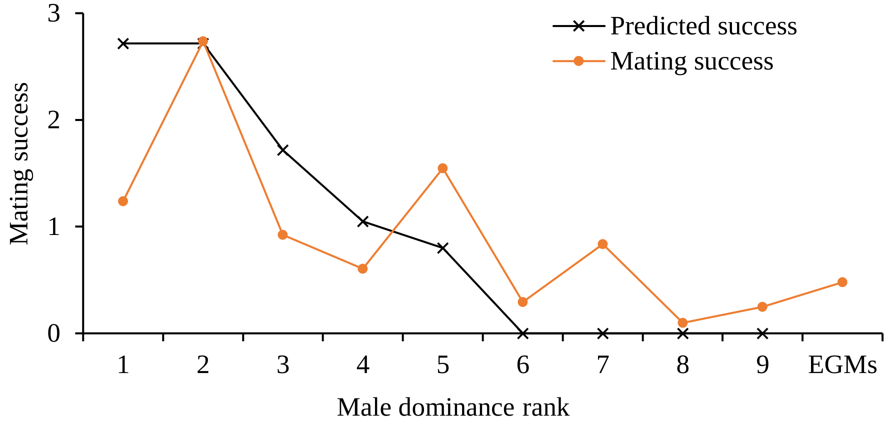


Figure 4.2 Comparisons of the predictions of the PoA model (male's predicted success based on female synchrony) with male's observed mating success (proportion of copulations) and observed reproductive success (number of infants sired) from Data Set 1 before (9a) and after (9b) rank change Ting-Khao, and during the entire study period (9c) in relation to male dominance rank and EGMs.

(10a) Before rank change Ting-Khao



(10b) After rank change Ting-Khao



(10c) Entire study period

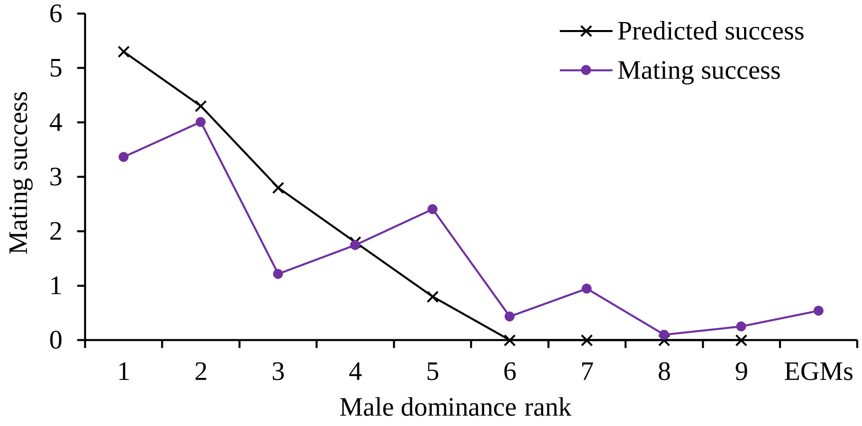


Figure 4.3 Comparisons of the predictions of the PoA model (male's predicted success based on female synchrony) with male's observed mating success (proportion of copulations) from Data Set 2 before (10a) and after (10b) rank change Ting-Khao, and during the entire study period (10c) in relation to male dominance rank and EGMs.

CHAPTER 5

MALE MATING TACTICS IN WILD NORTHERN PIG-TAILED MACAQUES: FACTORS AFFECTING ALPHA MALE MONOPOLY

5.A. Introduction

An essential question in studies of primate sexual selection is to assess proximate factors affecting male reproductive success. In multi-male group-living mammals, males compete with other males for access to females and to copulate when females form a cluster (Dixson & Anderson, 2002). Comparative analyses have shown a positive correlation between male dominance rank and reproductive success with a reproductive advantage for high-ranking males in mammals (Ellis, 1995), including primates (this study; Alberts, 2012; Cowlishaw & Dunbar, 1991; Dixson, 2012; Majolo et al., 2012). These studies suggest a major impact of dominance rank on male reproductive success. While most mammals seem to follow this general pattern (Ellis, 1995), the ability of the alpha male to control access to females also shows great variation among primates (e.g., Kutsukake & Nunn, 2006; van Noordwijk & van Schaik, 2004).

In primates living in multi-male groups, one main factor that is believed to affect the relationship between male dominance rank and reproductive success is the degree of female reproductive synchrony (female synchrony), which is a measure of the number of females simultaneously sexually receptive in a group (Paul, 2002; Setchell, 2008; van Noordwijk & van

Schaik, 2004; van Schaik et al., 2004). As introduced in Chapter 4, the Priority-of-Access model (PoA model) (Altmann, 1962) is usually used to predict the effect of female synchrony on the relationship between male dominance rank and reproductive success (see Kutsukake & Nunn, 2006). Together with other studies (Alberts et al., 2006; Boesch et al., 2006; Dubuc et al., 2011; Engelhardt et al., 2006; Setchell et al., 2005a; Sukmak et al., 2014), my findings detailed in Chapter 4 indicated that the PoA model correctly predicted the significant relationship between male mating/reproductive success and dominance rank. However, the mating and reproductive skew towards the alpha male predicted by the model was overestimated, and the overall predicted sharing of copulations/paternity among lower-ranking males was underestimated compared to what my analyses revealed.

Several proximate factors have been proposed to explain the residual variation from the mating/reproductive success predicted by the PoA model. Among those are energetic constraints on males, surreptitious copulations, stability of the male dominance hierarchy, males' opportunity for sexual coercion, the number of male competitors within a group, presence and number of extra-group males gaining access to a group, and the intensity of female mate choice (Alberts, 2012; Alberts et al., 2003; Bissonnette et al., 2011; Port & Kappeler, 2010; Young, Hähndel, et al., 2013). Indeed, higher-ranking males may be more limited in time and energy that they can invest into mate-guarding receptive females than the PoA model assumes (Alberts et al., 2006; Engelhardt et al., 2006). Among non-seasonally breeding primates (e.g., long-tailed macaques, *M. fascicularis*, Engelhardt et al., 2006), where female synchrony is less common, high-ranking males will often attempt to monopolize a female during her receptive period by forming a consortship with her (i.e., mate-guarding the female). In contrast, among seasonally breeding species, females are often synchronized in their receptive periods, which reduces the top-ranking male's ability to monopolize females and allows lower-ranking males to copulate and reproduce with females (e.g., Barbary macaques, *M. sylvanus*, Young, Majolo, et al., 2013).

Lower-ranking males may also develop alternative reproductive tactics aiming at circumventing the main strategy of using male-male dominance to gain access to and monopolize receptive females (Setchell, 2008; Young, Majolo, et al., 2013). Surreptitious copulations (i.e., when a subordinate male copulates with a female out of sight of dominant males) are part of subordinate males' alternative mating tactics and have been recorded widely in species, such as mandrills (*Mandrillus sphinx*, Setchell, 2008), baboons (*Papio sp.*, Byrne, Whiten, & Henzi, 1990; Smuts, 1985), patas monkeys (*Erythrocebus patas*, Ohsawa et al., 1993), rhesus macaques (*Macaca mulatta*; Overduin-de Vries et al., 2012; Smith, 1994), and Japanese macaques (*M. fuscata*, Inoue & Takenaka, 2008) (reviewed by Setchell, 2008). Several studies have confirmed that surreptitious copulations can result in fertilization, e.g. in patas monkeys (Ohsawa et al., 1993), rhesus macaques, (Berard et al., 1994; Manson, 1996), and langurs (*Semnopithecus entellu*s, Launhardt et al., 2001). Lower-ranking males may also form long consortships with a receptive female by traveling alone with her and copulating away from other members of the group, as a form of "stealing" away the female from dominant males (e.g., chimpanzees, *P. troglodytes*, Wroblewski et al., 2009).

The presence of extra-group males (EGMs) is also expected to influence male reproductive skew in a group. As for lower-ranking males, EGMs may use short consortships as an alternative mating tactic. They may linger at a group's periphery and "sneak" a copulation, which means a fast (i.e., <1min) copulation with a female out of view of resident males (e.g., Berard et al., 1994; Manson, 1996; Ohsawa et al., 1993; Setchell, 2008; Sprague, 1991b). The success of alternative mating tactics of EGMs has been verified by extra-group paternity, which so far has been shown to range from as little as 7% of offspring sired by EGMs in savanna baboons (*P. cynocephalus*, Alberts et al., 2006) to as much as 61% in Japanese macaques (Inoue & Takenaka, 2008). However, yet little is known about EGM's mating tactics and factors such as female synchrony affecting extra-group paternity among primates (Ruiz-Lambides et al., 2017).

In this chapter, I investigated how male mating tactics influenced male-female consortship formation, male sexual behaviors, and how the presence of EGMs affected the relationship between male dominance rank, mating success, and reproductive success in male northern pig-tailed macaques (*M. leonina*) at Khao Yai National Park (KYNP), Thailand. Northern pig-tailed macaques live in large multi-male, multi-female groups with a female-biased adult sex ratio. In Chapter 3, I was able to show that this study group of northern pig-tailed macaques falls into the category of moderately seasonally breeding primates, highlighting a temporal overlap among receptive periods of females. Furthermore, results of the test of the PoA model (see Chapter 4) confirmed that as female synchrony increases, the alpha male's ability to control access to all females decreases. Even though the high-ranking males controlled most of the matings and paternity in the group, the PoA model overestimated the ability of high-ranking males to control access to females, and underestimated alternative male mating tactics by lower-ranking males and EGMs (see Chapter 4).

In this chapter, I tested the hypothesis that mating tactics among males would differ based on their migration status and dominance rank (H_1). Due to priority of access by high-ranking males to receptive females, I predicted among resident males that: (P_{1a}) frequency and duration of male consortships would correlate inversely with dominance rank (i.e., the highest-ranking male carries the lowest numerical rank value while the lowest-ranking male carries the greatest numerical value), so that highest-ranking males would have the most and longest consortships;

and (P_{2a}) duration of copulations would be correlated inversely with dominance rank, so that the highest-ranking males would have the longest copulations. I also predicted that (P_{3a}) when females are simultaneously receptive, lower-ranking males would monitor consortships between higher-ranking males and receptive females to access females through surreptitious copulations. Likewise, I predicted that (P_{4a}) EGMs would access receptive females through surreptitious copulations when females are simultaneously receptive.

5.B. Methods

5.B.1. Study site and subjects

The study site is located in the Mo Singto area in KYNP, northeastern Thailand (2,168 km^2; 14°26′42″ N, 101°21′56″ E; 130 km NE of Bangkok). The larger Mo Singto area is around 10 km^2 (José-Domínguez, Huynen, et al., 2015; Reichard et al., 2012) and is covered by a seasonal tropical forest, with an altitudinal range of 730-890 m above sea level (Kitamura et al., 2005; Kitamura et al., 2008; Reichard et al., 2012; Smitinand, 1989). KYNP can be characterized by a rainy season (May-October), a cold season (November-February), and a hot season (March-April) (for further details, see 2.C. Study Site).

For this chapter, systematic data were collected from Sep. 2015-Dec. 2016 in CH group, which was entirely wild-feeding (José-Domínguez, Huynen, et al., 2015; José-Domínguez, Savini, et al., 2015). I divided the study into two phases: Phase I—a two-month period (Sep.-Oct. 2015)—was used to identify all subadult and adult individuals of the group. Phase II—a 14-month period (Nov. 2015-Dec. 2016)—was the main behavioral data collection period (for further details, see 2.E.1. Timeline for Data Collection).

During Sep. 2015-Dec. 2016, CH group varied between 60-75 individuals and was composed of 6-10 resident males (3-5 adult males and 3-6 subadult males), 0-7 immigrant males (4 adults, 3 subadults), 18-24 adult females, and an estimated 35-45 immature individuals (see Figure 3.1). Observations of 14 extra-group males (11 adults, 3 subadults) in CH's vicinity were scattered throughout the study period (III.C.1.d. Extra-group Males). I differentiated three types of males: 1) resident males, considered members of the group who interacted daily with other group members according to dominance rank; 2) immigrant males, who stayed in the group for at least seven days, were seen daily, mostly at the periphery of the group, and occasionally interacted with group members; and 3) extra-group males (EGMs), who were usually seen at the periphery of the group or were absent during most observation days, and rarely interacted with group members. More details of how these types were identified are available in Chapter 3 (3.B.2.c. Male Migration Status).

5.B.2. Behavioral data collection

One to three observers (CC-B, CB, MR, NL, and/or FT) recorded behavioral data during females' receptive periods throughout Study Phase II (four to six days a week, 7 am-6 pm; for further details, see 2.E.3. Behavioral Data Collection). From Aug.-Dec. 2016, only FT collected data. Continuous focal sampling (focal sampling) (Altmann, 1974; Martin & Bateson, 2007) were collected for 14 receptive periods (5 in 2015, 9 in 2016) of 14 females (3 nulliparous, 11 parous), at one- to three-day intervals with a total of 104.2 hours in 2015 and 454.6 hours in 2016 (for further details, including definition of female's receptive period, see 4.B.2. Behavioral Data Collection). In addition, *ad-libitum* data (Altmann, 1974; Martin & Bateson, 2007) provided information on 12 receptive periods (8 in 2015, 4 in 2016) of 10 parous females. Focal sampling was also conducted on males (four adults, one subadult) every one to three days with a total of 59.5 hours in 2015 and 42.3 hours in 2016 (see Table 4.2) between Nov. 2015-Mar. 2016. From April 2016 until the end of the study, males could not be followed during the mating period as more than two females were simultaneously receptive and only these females were observed. During focal follows, all behavioral data were recorded on an iPad mini 4 using the Animal Behavior Pro iOS App (Newton-Fisher, 2012). Using a random number generator, focal individuals were chosen randomly to achieve an unbiased, equal daily observation time for each focal animal.

All occurrences of sexual behaviors (copulation, ejaculatory copulation; see Table 4.3 for definitions) and the identity of the focal individual's partner were recorded during focal follows and *ad-libitum* observations throughout the day. In addition, during each focal follow, instantaneous data on spatial proximity between the focal female and other adult males (contact, within 2 m, 5 m, 10 m, and more than 10 m) were recorded using instantaneous sampling at 2-min intervals (adapted from Garcia, Shimizu, & Huffman, 2009). These data were used to determine consortship frequencies and durations. Lastly, aggressive and submissive behaviors were recorded during focal sampling and *ad libitum* sampling. Male-male and female-female agonistic behaviors were used to determine male and female dominance rank positions.

5.B.3. Male dominance hierarchy

The male dominance hierarchy was established from all dyadic interactions of aggression and submission between two males. Bidirectional agonistic behaviors, in which two individuals aggressed each other, were not included in this analysis. Only subadult males, who engaged in agonistic interactions with adult males and copulated with receptive females, were included in the male dominance hierarchy. Immigrant males and EGMs interacted rarely with the resident males, therefore they could not be included in the dominance hierarchy. The corrected, normalized David's scores was used to assess dominance rank (de Vries et al., 2006), using the package "steepness" (Leiva & de Vries, 2014) in R v. 3.5.1 statistical software package (R Development Core Team, 2018) based on a sociometric matrix of wins calculated for each dyad (see 3.B.3. Dominance Hierarchy). Male dominance hierarchy was divided into three categories: high-ranking males (alpha and beta males), middle-ranking males (ranks 3-4), and low-ranking males (ranks 5-9).

I witnessed two male take-overs of the alpha male position, each by an immigrant male (see 3.C.3. Take-overs of Male Dominance). The first take-over occurred in December 2015 when immigrant male Farang ousted the alpha male Ting (rank change Ting-Farang), who had been the top-ranking male since 2012 (pers. comm., José-Domínguez) but remained in the group as the beta male after the take-over. However, Farang disappeared only about a week after he had attained the alpha male position. Ting regained his alpha male position after Farang left (rank change Farang-Ting). The second take-over occurred in April 2016, when male Khao immigrated and replaced the alpha-male Ting (rank change Ting-Khao); again, Ting stayed in the group but dropped to the third-ranking male position.

5.B.4. Male-female consortships

Adapted from previous studies on rhesus macaques (*M. mulatta*, Berard et al., 1994; Brauch et al., 2008) and Barbary macaques (*M. sylvanus*, Brauch et al. 2008), I defined a consortship as a male and a female: 1) being in persistent close proximity (<10 m, one of them following the other); and 2) copulating during the day. A consort started when the male/female approached within 10 m and ended when either copulated with another individual, when spatial proximity terminated (i.e., >10 m apart), or when one of the individuals ceased following the other for more than ten consecutive minutes. A consort was disrupted when a male and a female were forced to end their consort due to an interaction with another male (passive approach, agonistic behaviors).

From observations during each female's receptive period, the percent value of consortships achieved by a male was calculated as the sum of the duration of all consortships achieved by the male during the female's receptive period, divided by the total duration of consortships achieved by all males during the female's receptive period. The total percent value of consortship achieved by a male was calculated as the sum of all consortship proportions of a male over all females' receptive periods. I then examined the relationship between male-female consortship (average duration, percentage) and dominance rank using Spearman correlation test. These measures of consortship duration and percent were intended as quantitative measures of "female preference." I assumed that consortships that lasted longer and would make up a greater proportion of a female's overall consortships would reflect a greater interest in or acceptance of a particular male by a female. Finally, I tested whether high-ranking/adult males were more often involved in consortships and in longer consortships than middle- and low-ranking/subadult males using Mann–Whitney test and Kruskal-Wallis rank sum test. I also looked at the effect of consortship interruptions by higher-ranking males between adult and subadult resident males using Z-test (two-sample test for equality of proportions).

5.B.5. Mating patterns among resident males and EGMs

Because northern pig-tailed macaques are multiple mount ejaculators, I calculated the duration of copulations and the number of mounts per copulation of all resident males and EGMs. Consequently, only complete copulations (i.e., when I recorded the mount series from beginning to end) from observations during each female's receptive period were used to do these calculations. I compared the copulation duration and the number of mounts per copulation between adults and subadults among resident males using a Mann-Whitney U-test. I looked at the effect of interruption of consortships by higher-ranking males between adult and subadult resident males using Z-test (two-sample test for equality of proportions). To look at whether subadult males have more pressure to copulate quickly with females to avoid interruption by adult males, I also examined whether subadults were more involved in single-mount ejaculatory copulations than adults among resident males. Due to the low number of copulations observed with EGMs, no comparative statistical test with resident males could be conducted.

5.B.6. Statistics

All statistical tests were calculated with the R v. 3.5.1 statistical software (R Development Core Team, 2018). I used the package "pspearman" (Savicky, 2014) for Spearman correlation test, and the package "MASS" (Venables & Ripley, 2002) for remaining tests. All tests were two-sided, except *Z*-tests that were one-sided. The significance level was set to $p<0.05$ for all statistical tests.

5.C. Results

5.C.1. Receptive female synchrony and mating partners

During Study Phases I and II (Sep. 15-Dec. 16), 26 receptive periods of 14 females were recorded (before/after rank change Ting-Khao: 14/12; see Figure 3.1 and Table 4.1), including 15 receptive periods of 13 females recorded through focal sampling (before/after rank change Ting-Khao: 6/9 receptive periods; see Table 4.1). Nineteen complete female receptive periods were recorded lasting on average 24 days. The mean number of simultaneously receptive females on a given day of a receptive period was 2.4 females, with a maximum of 5 females (before/after rank change: mean 2.7/2.4 females, min. 1/1, max. 5/5 females).

5.C.2. Male-female consortships of resident males

Among resident males, I observed 489 male-female consortships lasting 373 hours total. Consortship duration was often incomplete because: 1) a consorting pair left the main part of the group and ranged out of sight of the observer, or 2) a consort lasted longer than a focal follow.

All ten resident males formed consortships with receptive females. All consortships with middle- and low-ranking males occurred out of sight of dominant males. There was a significant negative correlation between male dominance rank and the proportion of consortships per female's receptive period (r_s=-0.43, p<0.001; Table 5.1). High-ranking males (i.e., alpha and beta males) had a greater proportion of consortships than middle- and low-ranking males and were able to control 62.4% of all observed consortships. Likewise, dominance rank was significantly negatively correlated with consortship duration (r_s=-0.27, p<0.001; Table 5.1), such that high-ranking males had consortships of the longest durations. The proportion of consortships per female's receptive period was significantly different among the three categories of male dominance rank ($\chi^2(2)$=23.3, *p*=0.001). High-ranking males were significantly more often engaged in consortships (mean±SD, 25.3±23.2% of the consortships per female's receptive period) than middle- (11.5±13.5%, pairwise comparisons: *p*=0.013) and low-ranking males (3.1±4.4%, pairwise comparisons: p<0.001; Table 5.1). Middle-ranking males were also significantly more often engaged in consortships than low-ranking males (pairwise comparisons: *p*<0.001). However, the proportion of consortships per female's receptive period greatly varied within each category of male dominance rank, with high-ranking males ranging from 0-82%, middle-ranking males ranging from 0-69%, and low-ranking males ranging from 0-16%.

Similarly, the average consortship duration was significantly different among the three categories of male dominance rank ($\chi^2(2)$=44.4, *p*<0.001). High-ranking males were significantly engaged in longer consortships (53.5±44.1 min) than middle- (32.9±32.3 min, pairwise comparisons: *p*<0.001) and low-ranking males (30.9±30.9 min, pairwise comparisons: p<0.001; Table 5.1). Indeed, 23.4% of consortships of middle- and low-ranking males were interrupted by a higher-ranking male. However, consortship duration greatly varied within each category of male dominance rank, with high-ranking males ranging from 6-275 min, middle-ranking males ranging from 6-253 min, and low-ranking males ranging from 6-140 min.

High-ranking males were the only males observed consorting with receptive females for more than three hours on eight occasions (1.6% of consortships). During one female's conceptive cycle, the beta male Snoopy was involved in daily long and close consortships with female Kay for a month. The beta male controlled 81.6% of her consortships with more than 25% of consortships lasting more than 2 hours. No other account of such extended consortship formation during a female's receptive periods was observed.

In 32.9% of consortships interrupted by a higher-ranking male (*n*=83), the lower-ranking male continued to follow the new consorting pair as a secondary follower (i.e., remaining in sight). In 61.5% of these consorts (*n*=26), lower-ranking males remained in the vicinity of the consorting pair until the dominant male left the receptive female, upon which they began a new consortship with copulations with the receptive female.

When dividing the data into a period of before and after the rank change Ting-Khao, no significant difference was found in the pattern of consortship among the category of male dominance rank. However, there was a difference observed between the two alpha males. Ting as alpha male controlled 36%±27% (mean±SD) of consortships per female receptive period while Khao as alpha male controlled only 18%±19%. It remained unclear if Khao was less interested in consortships with females or receptive females were less willing to accept his consort compared to Ting.

Among resident males, consortships of adults (dominant over subadults) were different from those of subadults. Adult males were significantly more engaged in consortships (U=178, p<0.001) and in significantly longer consortships than subadult males (U=28854, p<0.001). Adult males controlled on average 60.7%±27.4% of consortships per female receptive period with an average duration of 50.9±43.4 min, while subadult males controlled 24.6%±18.4% with an average duration of 25.3±23.0 min (Table 5.2). Consortships with subadult males were also significantly more often interrupted by an adult male (36.0% of subadult male consortships, *n*=386) than consortships with adult males (10.9% of adult male consortships, *n*=103; $\chi^2(1)$=35.8, p<0.001).

Finally, in 12 of 15 receptive periods (80%) for which data were available for both mating success and consortships (using data from Chapter 4), the male with the highest mating success with the receptive female also achieved the highest proportion of consortships with her. Similarly, in four out of seven receptive periods (57%) for which consortship and paternity data were available (using data from Chapter 4), the male who sired the female's offspring also had the highest consortship proportion with her. It appeared that extended consortships with a receptive female increased the male's chances to copulate with a female and sire her offspring.

5.C.3. Mating patterns of resident males

Among resident males, I observed 297 complete copulations (observed from beginning to end), including 131 ejaculatory copulations (44.1% of observed complete copulations). Male northern pig-tailed macaques in my study group were primarily multiple mount ejaculators, as previously described in the literature (Carlson, 2011; Feeroz, 2003), with an average of 7.5±4.0 mounts preceding ejaculation. Ejaculatory copulations lasted on average 24.9±18.1 min. A male could be seen to ejaculate during the first mount with a female, but this pattern was unusual accounting for only 6 of 212 (2.8%) observed copulations.

Adult males ended copulations significantly more often with an ejaculation (60.6%) compared to subadult males (41.0%; $\chi^2(1)=6.17$, $p=0.007$). Ejaculatory copulations of adult males were also significantly longer (26.9±18.6 min) than those of subadult males (16.5±12.8 min; $U=1638.5$, $p=0.004$; Table 5.2, Figure 5.1). The number of mounts per ejaculatory copulation was significantly higher in adult males (8.0±4.2 mounts/ejaculatory copulation) compared to subadult males (5.4±2.3 mounts/ejaculatory copulation; $U=1685$, $p=0.003$; Table 5.2, Figure 5.1). This difference might have been the result of higher-ranking adult males interrupting more often lower-ranking subadult males' ejaculatory copulations (20.5% of their ejaculatory copulations) than lower-ranking subadult males interrupting higher-ranking adult males’ ejaculatory copulations (4.8%). Perhaps lower-ranking subadult males’ ejaculatory copulations were shorter out of fear of being interrupted by higher-ranking adult males. Single mount ejaculations were also observed in 5.8% of subadult males’ ejaculatory copulations (3 out of 52) but only in 1.9% of adult males’ ejaculatory copulations (3 out of 160).

After an ejaculatory copulation with a female or after a copulation with a female interrupted by a high-ranking male, a middle- or low-ranking male (adult or subadult) often attempted to interrupt mounts between the high-ranking male (alpha or beta male) and the female by harassing the high-ranking male. The lower-ranking male would closely approach and scream with a high pitch at the high-ranking male in the action of mounting the female. The high-ranking male would either ignore or face-threat the lower-ranking male while continuing mounting the female, or end mounting the female and chase the lower-ranking male away. Middle- and low-ranking males attempted to interrupt 58 mounts between a high-ranking male and a female during 23 ejaculatory copulations of 6 receptive females. Middle- and low-ranking males successfully interrupted 79.3% of those ejaculatory copulations, and 30.4% of those ejaculatory copulations (7 out of 23) did not end with the high-ranking male ejaculating because the high-ranking male or the receptive female left the dyad after several mounts had been interrupted by the lower-ranking male.

5.C.4. Male-female consortship and mating pattern of EGMs

Fourteen EGMs (11 adults, 3 subadults) were seen at the periphery of CH group during the study (see 3.C.1.d. Extra-group Males and Figure 3.1). For EGMs, it was unknown if they were part of a different multi-male, multi-female group or if they belonged to an all-male band, although no all-male band was ever encountered in the forest. However, on several occasions, unknown mature male northern pig-tailed macaques were seen foraging on their own, suggesting that EGMs seen in CH's vicinity may have been living semi-solitarily. A higher number of EGMs (average of four males/month, range 3-5) was observed at CH's periphery during the three-month mating peak of 2016 compared to the rest of the study period (average of one male/month, range 0-3) and to the one-month mating peak of 2015 (1 male; Figure 5.2). EGMs were seen at the periphery of the group for only a few days or for more than a month, but with short gaps of one- to three days of absence of observations because: 1) no observer was in the field; 2) an EGM was not noticed; or 3) an EGM was in fact absent.

EGMs were observed interacting with receptive females, juveniles, and subadults through affiliative and agonistic behaviors, but only behaved agonistically towards adult males. When approaching the periphery of the group, EGMs would either be quiet or perform tree-shaking branches as a display. Seven EGMs were observed in 24 consortships with females (4.7% of consortships) with an average duration of 45.4±44.0 min (Table 5.1). Similar to consortships with middle- and low-ranking males, consortships with EGMs occurred at the periphery of the group, away from resident males.

On four occasions, the consortship with an EGM was interrupted by a resident adult male. However, one consortship between Chuan and Olan occurred in sight of resident adult males. Chuan was showing dominant behaviors (chase, face threat, and branch-shaking) towards the resident adult males, who attempted to interrupt the consortship on several occasions. Chuan also interrupted two copulations between Olan and the third- and fourth-ranking adult males Ting and Kanhuh, respectively, by chasing the males away and then started a new copulation with Olan.

In addition, on nine occasions, I witnessed five EGMs (Aran, Boo, Chuan, Drogo, and Manu) being actively approached by a receptive female after she temporarily left or travelled to the periphery of the group. Further, based on *ad libitum* observations, receptive female Tao left the group for more than two weeks (i.e., she was not observed in CH group during that time) and she was seen in long-lasting consortships with EGMs Manu and Chuan on three different days. Likewise, females Lawan and Baan were often absent from the group during their receptive period, but only Lawan was observed copulating with EGMs at the periphery of the group and during her absences from the group. The observations of Tao and Lawan copulating/consorting with EGMs away from the rest of group were witnessed by observer FT when he was looking for the group or walking back to the field station house.

Among EGMs, I observed 11 complete copulations including five ejaculatory copulations (45.4 % of observed complete copulations). One EGM ejaculated during the first mount with a female (1 out of 5 ejaculatory copulations). Ejaculatory copulations of EGMs lasted 16.3±8.9 min, which was almost identical in duration to the ones of resident subadult males (16.5±12.8 min) but shorter than the ones of resident adult males (26.9±18.6 min; Table 5.2). However, the number of mounts per ejaculatory copulation of EGMs (6.8±3.0 mounts/ejaculatory copulation) was closer to the one of resident adult males (8.0±4.2 mounts/ejaculatory copulation) and higher than the one of resident subadult males (5.4±2.3 mounts/ejaculatory copulation; Table 5.2). None of the observed ejaculatory copulations with EGMs was attempted to be interrupted by a resident male.

5.D. Discussion

Among multi-male, multi-female living-primate groups, males usually engage in direct contest competition for access to mates (Clutton-Brock, 2004). Based on their fighting abilities, males who are the strongest can reach the top of the hierarchy and are thus expected to control access to receptive females, which in turn suppress lower-ranking males' mating efforts and force them to follow alternative mating tactics. In my study, high-ranking males (alpha and beta males) guarded receptive females through longer and more frequent consortships than other resident males. Because high-ranking males often interrupted lower-ranking males' consortships, middle- and low-ranking males were forced to access females through shorter consortships and surreptitious copulations out of sight of high-ranking males. Middle- and low-ranking males were also observed monitoring higher-ranking males' consortships to consort and copulate with the receptive females after the higher-ranking male left. EGMs were also able to access females at the outskirt of the group through short and sneaky copulations. Thus, this study highlights the importance of alternative male mating tactics by middle- and low-ranking males and EGMs, generally not considered in the PoA model.

Male macaques may gain access to receptive females by forming consortships and thereby effectively preventing other males from being able to consort or copulate, so called mate-guarding. I found that consortships were significantly more frequent (62% of consortships) and longer (lasting up to 3-4 hours) for the high-ranking males. A significant dominance rank effect on male mate-guarding activity found in this study and other studies (e.g., savanna baboons, Alberts et al., 2006; Assamese macaques, Ostner, Heistermann, & Schülke, 2011; long-tailed macaques, *M. fascicularis*, Engelhardt et al., 2006) suggest that this tactic of access is disputed among males (Sukmak et al., 2014). Mate-guarding tactic increased males' mating success because males who consorted more often with receptive females had a higher mating success (Alberts et al., 2006; Berard et al., 1994; this study).

Mate-guarding is considered time consuming and energy-limited for males (Alberts, Altmann, & Wilson, 1996; Packer, 1979). Indeed, it is always challenging to meet one's own energy requirements and feed sufficiently while simultaneously successfully keeping other males away from a female (Alberts et al., 2006). If a male loses too much energy reserve while mate-guarding a receptive female, he may be disadvantaged to start mate-guarding again once another female becomes receptive (Alberts et al., 2006). Furthermore, mate-guarding is not a perfect solution for males to monopolize receptive females because high performance of consortship does not necessarily translate directly into siring an offspring (Sukmak et al., 2014; this study). In my study, for instance, the beta male Snoopy mate-guarded receptive female Kay almost daily for a month but he mate-guarded receptive female Em, who was receptive at the same time as Kay, on only a few occasions. While Snoopy mate-guarded Kay, Em was either mate-guarded by the third- or fourth-ranking males but not the alpha male Khao, who did not show much interest in this female or any other receptive females at that time (pers. obs.). The amount of time and energy that Snoopy spent in the consortship with Kay may have exhausted him and affected his ability to mate-guard other receptive females. In the end, however, Snoopy did not even sire Kay's offspring nor Em's (see Table 4.6).

Because of limited time and/or energy, high-ranking males may not be able to permanently guard the receptive females and prevent lower-ranking males from copulating. Middle-ranking males (adults and subadults) and, to a greater degree, low-ranking males (subadults) were engaged in shorter consortships and copulations and also used more single-mount ejaculations (but still at a low rate) than high-ranking adult males. Copulations between middle-/low-ranking males and receptive females always occurred away from high-ranking males, and in many occasions, at the periphery of the group. These results suggest that middle- and low-ranking males are more furtive and surreptitious when copulating with receptive females to avoid being interrupted by a higher-ranking male. Indeed, middle- and low-ranking males were often interrupted by a higher-ranking male (23.4% of their consortships).

Consortships by middle- and low-ranking males found in my study may be similar to the consortship tactics found in chimpanzees (Wroblewski et al., 2009), in which low-ranking males use consortships as a way to “steal” females away from high-ranking males. This middle- and low-ranking male tactic (furtive copulations, surreptitious consortships) was successful for at least one subadult male, Naam, who sired one offspring in my study (see 4.C.2.d. Resident Males’ Paternity), and also in rhesus macaques (Berard et al., 1994), Japanese macaques (Soltis et al., 2001), and to a lesser degree, in savanna baboons (Alberts et al., 2006). Forest setting with dense vegetation, such as the one described in this study (see 2.C. Study Site), may offer a more effective environment to conceal copulations and consortships from higher-ranking males than the relatively open habitat in Amboseli of savanna baboons (Alberts et al., 2006). This habitat difference may explain the difference of middle- and low-ranking males’ mating and subsequent reproductive success among primates. However, even though the surreptitious mating tactic may be successful, it does not appear to be as effective as mate-guarding (Berard et al., 1994; Soltis et al., 2001; this study).

Thus, to maximize their reproductive success, resident males flexibly engage in alternative mating tactics depending on their dominance rank, as follows: 1) the top-ranking males engage in mate-guarding through long-lasting consortships; 2) the middle-rank males (adults and subadults) engage in mate-guarding when possible, combined with surreptitious copulations; and 3) the low-ranking males (subadults) are probably only able to sneak copulations out of sight of higher-ranking males.

Alternative mating tactics resulting in reproductive success are not only limited to resident males. During the mating peaks, at least seven EGMs (up to five males at a time) were observed at the periphery of the group. EGMs sired an unexpected high proportion of offspring in CH group (48%; see 4.C.2.e. EGMs' Paternity). EGMs were mostly observed during the mating peak, but only stayed for a few weeks, as none of them stayed for the entire mating peak. Despite the limited dataset, copulations between EGMs and receptive females were observed, but at very low rates compared to resident males. While EGMs' copulations were similar in duration to subadult resident males' copulations and, in most cases, occurred out of sight of resident males, EGMs' consortships were as long as adult resident males' consortships. In my study, EGMs were principally following receptive females at the edge of the group, up in the trees, in dense vegetation. These conditions explain why it is difficult, if not impossible, to follow and record mating behaviors of EGMs (see also 4.D. Discussion).

I identified two situations in which EGMs were able to copulate with a female: 1) when a female temporarily left or travelled to the periphery of the group and actively approached an EGM (female mate choice); or 2) when an EGM entered the group and established proximity with a receptive female without running away from resident males (male-male competition). First, I found several lines of evidence that female northern pig-tailed macaques showed preferences to copulate with EGMs, which may affect EGMs' reproductive success. In my study, on nine occasions, I witnessed receptive females who, after temporarily leaving the group, actively approached and copulated with EGMs. In addition, resident females Tao and Lawan, who went absent from the group most of the time during their receptive periods, maintained long-lasting consortships and repeatedly copulated with EGMs.

Consortships and copulations between resident females and EGMs have been reported for a wide range of Old World monkeys: Japanese macaques (Soltis, 2004; Sprague, 1991a, 1991b; Takahata, 1982; Wolfe, 1986), toque macaques (*M. sinica*, Keane et al., 1997), rhesus macaques (Brereton, 1981), long-tailed macaques (van Noordwijk, 1985b), blue monkeys (*Cercopithecus mitis*, Cords, Mitchell, Tsingalia, & Rowell, 1986; Cords & Rowell, 1986), and patas monkeys (Harding & Olson, 1986; Ohsawa et al., 1993). In those studies, evidence of an effect of female mate choice on EGMs' mating success were reported. For instance, as reported in my study, EGM Japanese macaques travelled quietly at the periphery of the group or performed tree-shaking branches, and waited for females to leave the group and approached them to copulate (Sprague, 1991b). In this same species, receptive females showed preference to copulate with sexually unfamiliar males (Wolfe, 1986) and avoided copulating with familiar males (i.e., males with whom females maintained spatial proximity and frequent exchange of grooming; Takahata, 1982).

Similar attractions of some females to EGMs as mates were also reported in long-tailed macaques (van Noordwijk, 1985b) and rhesus macaques (Brereton, 1981). In one group of blue monkey (Cords et al., 1986), it was even reported that resident females only copulated with EGMs and avoided copulations with resident males. Altogether, these observations indicate strong evidence of female mate choice towards EGMs, but further studies are much needed to investigate which characteristics (behavioral, morphological, or genetic) may attract females to copulate with those EGMs. For instance, female rhesus macaques show preference to copulate with darker red males (Dubuc, Allen, et al., 2014); thus the red ornament exhibited by male northern pig-tailed macaques could be used as well as a signal to sexually attract females (see Chapter 6).

While females may approach EGMs away from the group, EGMs may also actively approach receptive females that are in sight of resident males. Such approaches were followed by direct or indirect agonistic behaviors from adult and subadult males of the group. As suggested by Borries (2000), physical abilities or personality of resident males, especially of the alpha male, may influence the ability of EGMs to copulate with receptive females. In my study, resident males were agonistic towards EGMs, however variation of behaviors among resident males was noted. For instance, the number of EGMs at the periphery was higher during the mating peak when Khao was alpha male compared to when Ting was alpha male. Ting seemed more aggressive towards EGMs than Khao (pers. obs.). Such difference of behaviors could explain why more females were observed mating with EGMs during the mating peak after the rank change Ting-Khao.

Furthermore, on several occasions EGM Chuan directly approached a receptive female, while in sight of resident males who responded by agonistic behaviors. However, resident males were unsuccessful at chasing away Chuan, who stayed near the receptive female and copulated with her. Such behavior may show a super-dominance of this EGM over the resident males, but interestingly he showed no signs of aiming to take the alpha position. An effect of the individual persistence of EGM on their own reproductive success has also been shown in one group of *Cercopithecus* monkeys (Cords et al., 1986; Cords & Rowell, 1986; Harding & Olson, 1986). However, data on such behaviors in EGMs remains very limited.

Based on observations of Syke’s monkeys (*C. albogularis*), Henzi and Lawes (1988) proposed that EGMs may use two different tactics to access receptive females in multi-male groups: 1) hovering EGM tactic, where males monitor specific social group(s) to increase interactions with females and ensure copulation when these females become receptive; and

2) wandering EGM tactic, where males randomly search for and randomly attempt to copulate with any receptive female they encounter. Hovering EGMs are expected to wait for the mating peak to copulate, while wandering EGMs attempt to copulate throughout the year (Henzi & Lawes, 1988).

Based on my observations and because of the moderately seasonally breeding status of my study group (see Chapter 3), EGMs seems more likely to follow the hovering EGM tactic in northern pig-tailed macaques. Indeed, some EGMs (Aran, Ram, and Mii; see 3.C.1.e. Immigration and Emigration Records of CH Group's Males and Figure 3.1) were observed repeatedly at the periphery of the group, even when no female was receptive, suggesting that the same EGMs visited the group several times to monitor the females' reproductive status. Furthermore, in CH group, most females were simultaneously receptive over a three-month period, during which EGMs were more likely to access and copulate with receptive females (see Chapter 4). However, this mating peak may vary from year-to-year (see Chapter 3). Thus, EGMs who are monitoring repeatedly specific groups would be less likely to miss these groups' mating peaks and more likely to copulate with a female than EGMs who are monitoring random groups and would be more likely to miss groups' mating peaks. However, because information relative to behaviors of EGMs was limited outside of CH group, I can only speculate about EGMs' life and mating tactics. Thus, I cannot rule out that EGMs may follow the wandering tactic or may shift between both tactics. Long-term field studies on EGMs in northern pig-tailed macaques are needed to understand the factors affecting their patterns of migration among groups.

Previous studies have shown that female group size and the number of cycling females affect EGMs' influxes into one-male groups in species of langurs and *Cercopithecus* monkeys, specifically during mating periods (Cords, 1984; Cords et al., 1986; Cords & Rowell, 1986;

Harding & Olson, 1986; Henzi & Lawes, 1987; Henzi & Lawes, 1988; Tsingalia & Rowell, 1984), while these factors did not have an effect in a multi-male group of langurs (Borries, 2000). In Japanese macaques (Takahashi, 2001) and in Verreaux's sifakas (*Propithecus verreauxi*, Lawler, 2003), a relationship was found between extra-group paternity and operational sex ratio in a group (i.e., the ratio of receptive females to sexually mature males). Indeed, EGMs increased their chance of copulating with receptive females when the operational sex ratio was biased towards females, and consequently resident males could not control all receptive females. In my study, the presence of EGMs at the periphery of CH group was higher when more than two females were simultaneously receptive, i.e. during the mating peak.

Nevertheless, a review of 26 mammalian species found only a weak correlation between extra-group paternity and adult sex ratio (Isvaran & Clutton-Brock, 2007) and no significant correlation between extra-group copulations and group size in 13 primate species (van Noordwijk & van Schaik, 2004). More recently, a longitudinal analysis of causes of extra-group paternity in rhesus macaques revealed a significant positive correlation between extra-group paternity and proportion of females in larger groups, but not in smaller groups (Ruiz-Lambides et al., 2017). Thus, the relationships between adult sex ratio, group size, and extra-group paternity is variable and remains to be resolved.

However, it seems that female synchrony has a smaller effect on the density of EGMs in multi-male groups than in one-male groups. This difference of female synchrony's effect might be related to the two identified types of male visits into a social group: 1) EGMs can migrate into a social group and become resident males for weeks or months during the mating season (male influx, Borries, 2000); or 2) EGMs can remain at the periphery of a social group for days or weeks without immigrating into the social group (Sprague, 1991b).

Male influx has mostly been observed in one-male groups of blue monkeys (Cords et al., 1986; Tsingalia & Rowell, 1984), Syke's monkeys (Henzi & Lawes, 1987; Henzi & Lawes, 1988), redtail guenons (*C. ascanius*, Cords, 1984; Jones & Bush, 1988; Struhsaker, 1977), patas monkeys (Chism & Rowell, 1986; Harding & Olson, 1986), and to a lesser degree, in multi-male groups of Hanuman langurs (Laws & Laws, 1984), ring-tailed lemurs (*Lemur catta*, Sauther, 1991), and Japanese macaques (Takahata et al., 1994). Semi-solitary EGMs remaining at a group's periphery have only been reported in multi-male groups of Barbary macaques (Mehlman, 1986), Japanese macaques (Furuichi, 1985; Huffman, 1987, 1991; Sprague, 1991a, 1991b, 1992; Yamagiwa, 1985), rhesus macaques (Brereton, 1981; Lindburg, 1969; Neville, 1968), and northern pig-tailed macaques (this study).

Thus, peripheral semi-solitary EGMs may be more common in multi-male groups where male-male competition is high. Indeed, in this context, a male by himself may have better chances to access a receptive female than if he would be part of a male influx. This could explain why female synchrony has less effect on the density of semi-solitary EGMs in multi-male groups. On the other hand, male influx seems to be more likely in one-male groups, where male-male competition is reduced and all males that are part of an influx are more likely to be able to access receptive females. In this case, the density of a male influx may be more affected by female synchrony.

There are however some limitations associated with this study. As mentioned in Chapter 4, I used female's mating activity to determine female's receptive period because I could not determine female's fertile phase due to a lack of adequate hormonal data. Males, especially high-ranking males, should concentrate their mating effort during the female's fertile phase (i.e., during which copulation may directly lead to conception) (Engelhardt et al., 2006; Heistermann et al., 2008; Higham et al., 2012). The absence of precise knowledge of females' fertile phases in my dataset may have resulted in obscuring more subtle male mating tactics focused on just females' fertile period. For instance, high-ranking males may concentrate consortships and mating effort with a female more closely to her fertile period than I was able to show with this data set. However, this could be true for the alpha male in my study, but not for the beta male as none of his consorts and copulations led to conception.

In conclusion, in this chapter, I identified different male mating tactics in northern pig-tailed macaques, a moderately seasonal breeder. Surreptitious copulations, the presence of EGMs, and some evidence of female mate choice were identified as proximate factors affecting the association between dominance rank, mating success, and reproductive success in northern pig-tailed macaques. In this species, male access dominance through direct contest indicated strong male-male competition. Indeed, the alpha and beta males controlled the highest proportion of copulations and paternity by mate-guarding receptive females through long-lasting consortships. However, other males can be relatively successful through flexible alternative mating tactics. Indeed, middle- and low-ranking resident males and EGMs can ensure mating and reproductive success through mate-guarding when possible, combined with furtive, surreptitious copulations.

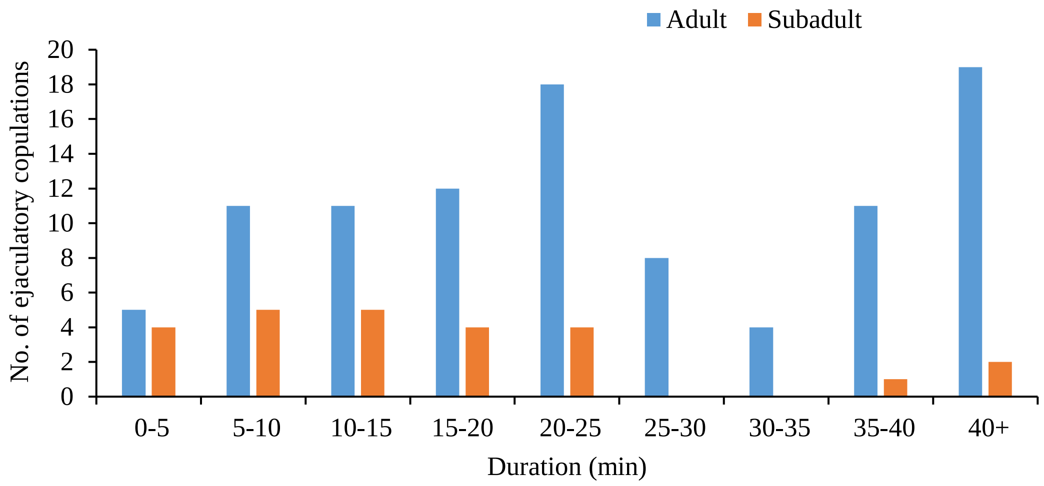
Table 5.1 Proportion and duration of consortships per female's receptive period in relation to male dominance rank and EGMs (*n*=489 consortships). Data are presented as mean±SD.

Category of male dominance rank	**Proportion of consortships (%)**	**Duration of consortships (min)**
High rank (rank 1-2)	25.3±23.2	53.5±44.1
Middle rank (rank 3-5)	11.5±13.5	32.9±32.3
Low rank (rank 6-9)	3.1±4.4	30.9±30.9
EGMs	6.1±9.7	45.4±44.0

Table 5.2 Proportion and duration of consortships, duration of ejaculatory copulations, and number of mounts per ejaculatory copulations per female receptive period in relation to male migration status (resident males vs. EGMs) and age status (adults vs. subadults) (*n*=489 consortships, *n*=131 ejaculatory copulations). Data are presented as mean±SD.

Male migration status	**Male age status**	**Proportion of consortships (%)**	**Duration of consortships (min)**	**Duration of ejaculatory copulations (min)**	**No. of mounts/ ejaculatory copulations**
Resident males	Adult males	60.7±27.4	50.9±43.4	26.9±18.6	8.0±4.2
	Subadult males	24.6±18.4	25.3±23.0	16.5±12.8	5.4±2.3
EGMs	Adult males	6.1±9.7	45.4±44.0	16.3±8.9	6.8±3.0

(1a) Comparison of the duration of ejaculatory copulations between adult and subadult males



(1b) Comparison of the number of mounts per ejaculatory copulation between adult and subadult males

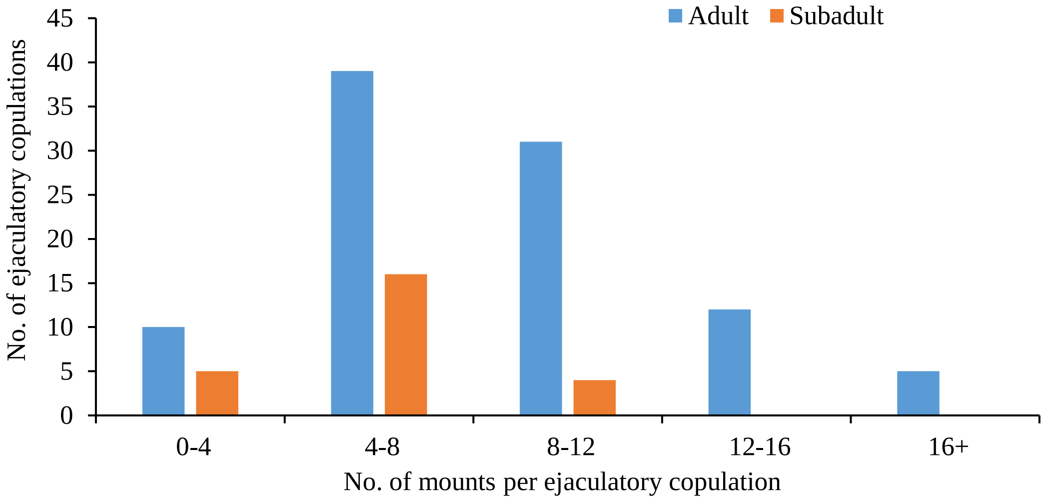


Figure 5.1 Comparisons of the duration of ejaculatory copulations and the number of mounts per ejaculatory copulations between adult and subadult males.

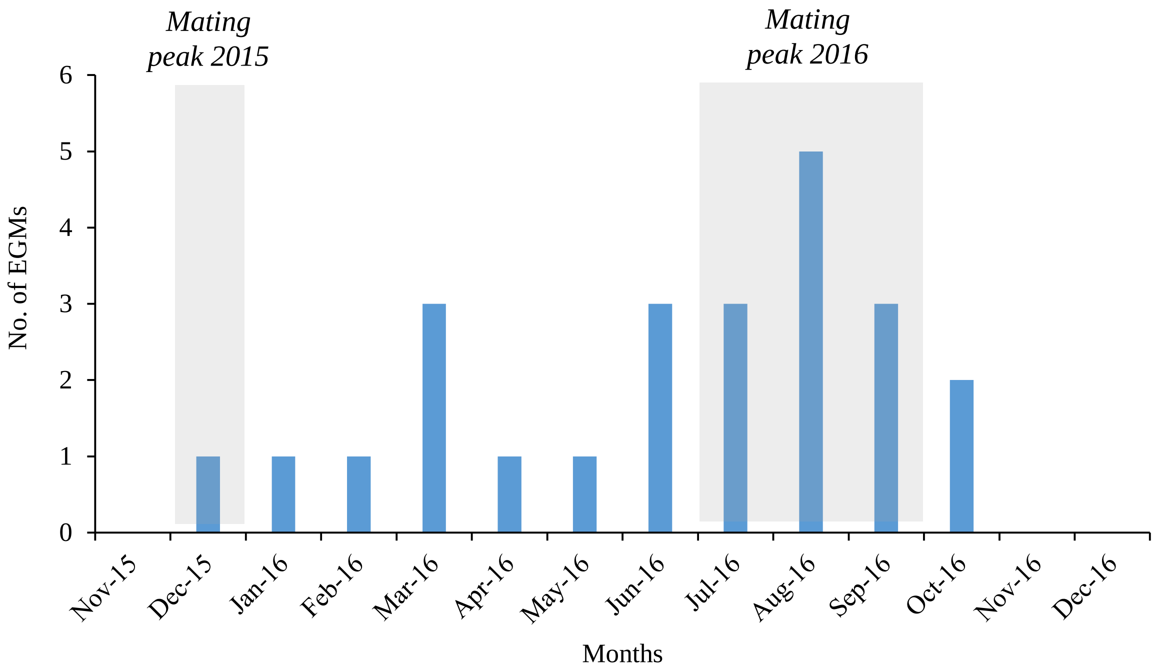


Figure 5.2 Monthly number of EGMs observed at the periphery of CH group from October 2015-December 2016.

CHAPTER 6

SECONDARY SEXUAL TRAITS IN WILD NORTHERN PIG-TAILED MACAQUES: MALE ORNAMENTATION IN RELATION TO SOCIAL RANK, MATING ACTIVITY, AND TESTOSTERONE

6.A. Introduction

Colorful ornaments of secondary sexual traits occur throughout the animal kingdom, from the brightly colored ocelli of the peacock's train to the bright nose of mandrills (Andersson, 1994; Darwin, 1871). In his classic book, *The Descent of Man, and Selection in Relation to Sex* (Darwin, 1871), Darwin realized that these non-utilitarian sexually dimorphic traits did not confer advantage over survival or direct production of offspring, but over competition for access to mates. Within sexual selection, Darwin recognized two fundamental driving forces: intrasexual selection, which results from mate competition among same-sex individuals, and intersexual selection, which results from mate choice between opposite sexes (Clutton-Brock, 2004; Darwin, 1871).

Male ornaments can take various forms and are usually more common than female ornaments (Andersson, 1994; Darwin, 1871). While weapons involved in fights evolved though intrasexual selection, non-utilitarian ornaments usually evolved through intersexual selection (Andersson, 1994; Darwin, 1871). The development of colorful ornaments is very common in birds (Hill & McGraw, 2006), lizards (Cooper & Greenberg, 1992), fishes (Houde, 2001), and insects (Bonduriansky, 2001), but is relatively scarce in mammals, which tend to be more characterized by the development of weapons (Clutton-Brock & McAuliffe, 2009; Emlen, 2008). This observation has led to the notion that female mate choice is less important in mammals than it is in other clades (Clutton-Brock & McAuliffe, 2009). However, male-male competition and female mate choice can affect the same male sexual traits by either reinforcing or opposing each other, with the former being more common (Hunt, Breuker, Sadowski, & Moore, 2009). For instance, a trait used to signal dominance to other males may equally be used by females as an indicator of male health and condition (e.g., Berglund, Bisazza, & Pilastro, 1996; Rasmussen & Schulte, 1998). In comparison to other clades, only a few studies in mammals have focused on both mechanisms of sexual selection and whether they may affect the same traits, partly because of the difficulty to separate the effect of each mechanism (Hunt et al., 2009).

Primates exhibit a wide array of conspicuous coloration on their skin and pelage (Bradley & Mundy, 2008), which are thought to be a product of sexual selection (Bradley & Mundy, 2008; Dixson, 2012). Such conspicuous coloration might have been promoted by both promiscuous mating systems (Andersson, 1994) and trichromatic vision in certain lineages of primates (Fernandez & Morris, 2007; though see Kamilar & Cooper, 2013). Indeed, the primate visual system most likely originally evolved to improve foraging performance at detecting red/orange food items against a background of dark green leaves (Lucas et al., 2003; Osorio & Vorobyev, 1996; reviewed in Surridge, Osorio, & Mundy, 2003). Comparative analyses suggested that trichromatic color vision evolved before red skin and red pelage and, once evolved, represented a pre-existing bias that promoted the evolution of red-orange traits in these species through sexual selection (Fernandez & Morris, 2007). The evolution of such conspicuous traits may have been further facilitated in promiscuous mating systems, in which sexual selection is thought to be stronger (Andersson, 1994). Among catarrhines, red male skin color is displayed on the most prominent body parts, e.g. the face, genitalia, and hindquarters of rhesus macaques (*Macaca mulatta*, Waitt et al., 2003) and mandrills (*Mandrillus sphinx*, Setchell & Dixson, 2001), or on the chest of geladas (*Theropithecus gelada*, Bergman & Beehner, 2008).

Most studies which focused on the adaptive function of colorful ornaments in primates have concluded that male displays are used as “badges of status” with dominant males exhibiting more colorful, i.e. redder skin color signals (e.g., mandrills, *M. sphinx*, Setchell & Jean Wickings, 2005; drills, *M. leucophaeus*, Marty et al., 2009; geladas, *T. gelada*, Bergman, Ho, & Beehner, 2009; crested macaques, *M. nigra*, Engelhardt, Neumann, Heistermann, & Perwitasari-Farajallah, 2008; black-and-white snub-nosed monkeys, *Rhinopithecus bieti*, Grueter, Isler, & Dixson, 2015). Coloration as a dominance signal is further supported by the observation that it can rapidly change with dominance take-over in mandrills and geladas. Most empirical data support the hypothesis that conspicuous signals of dominance should be favored in species that live in large groups where individuals may be limited to recognize or interact with all other group members (Bergman & Sheehan, 2013; Grueter et al., 2015; Setchell & Kappeler, 2003; Smith & Harper, 2003; e.g., geladas: Bergman et al., 2009; drills: Marty et al., 2009). Empirical studies have also led to the hypothesis of a close association between social status and red coloration in trichromatic primates (Khan, Levine, Dobson, & Kralik, 2011).

In addition to its function in male dominance signaling, male colorful ornaments may also function in attracting the opposite sex (e.g., mandrills, Setchell, 2005; rhesus macaques, Dubuc, Allen, et al., 2014). In mandrills, for example, while a strong correlation was found between male dominance rank and red nose coloration, receptive females also displayed more proceptive behaviors towards redder males, independent of males' positions in the male dominance hierarchy (Setchell, 2005). Because of coloration dual effect and a close correlation between male coloration, dominance rank, and mating success, it is often difficult to isolate the specific effect of female mate choice versus the effect of male-male competition (e.g., mandrills, Setchell, 2005; see also Dubuc et al., 2015). In rhesus macaques, where individuals show little sexual dimorphism in body mass and canine length, and mainly reach dominance through queuing, male red coloration was not found to correlate with dominance rank, but was still found to darken during the mating season (Dubuc, Allen, et al., 2014; Higham, Pfefferle, Heistermann, Maestripieri, & Stevens, 2013). The red male ornament appears to be attractive to females and darker red males received more sexual solicitations than pale pink males (Dubuc, Allen, et al., 2014). In addition, a recent study found that male facial redness may convey information on the competitive ability of a male to a rival (e.g., motivation to defend a mate) and may act as a signal of strength to mediate male conflicts or intimidate rivals during the mating season, similar to the function of a badge of status (Petersdorf et al., 2017). Thus, as in mandrills, the male colorful traits of rhesus macaques might be the result of both inter- and intrasexual selection and may convey reliable information of the signaler's general condition (Petersdorf et al., 2017).

At the proximate, physiological level, the red skin coloration in primates is related to epidermal blood flow in hairless areas of the face, genitals, and rump that is under control of sex steroid hormones (Rhodes et al., 1997). An experimental study on captive male rhesus macaques has demonstrated that testosterone acts indirectly via aromatization to estrogen, causing an increase of skin redness through action of estrogen-dependent receptors (Rhodes et al., 1997). These receptors are only located in the red skin area, which supports the idea that such coloration might be signaling information about both the competitive ability and the condition of the signaler to receivers of both sexes (Dubuc et al., 2015; Higham, Pfefferle, et al., 2013). Indeed, skin color is directly influenced by blood flow (haemoglobin skin concentration) and oxygenation (haemoglobin oxygenation saturation) (Zonios et al., 2001) and, consequently, can be affected by physiological or environmental factors, such as stress, health, and social relationships (Bradley & Mundy, 2008; Dixson, 2012). Furthermore, high levels of testosterone, which may be harmful to immune function (Folstad & Karter, 1992), have been linked to high stress levels (Braude, Tang-Martinez, & Taylor, 1999), increasing the risk of mortality (Marler & Moore, 1988). Therefore, the costs associated with producing testosterone should ensure that any signal controlled by testosterone should be honest (Muller, 2017). In male mandrills, testosterone levels are correlated with the intensity of red coloration and change in concert with color (Setchell et al., 2008). However, no such relationship was found in male rhesus macaques where red coloration did not correlate with dominance rank (Higham, Pfefferle, et al., 2013).

The costs associated with high testosterone levels may explain the lack of a consistent correlation between testosterone and dominance rank in male primates (Muller, 2017; Muller, Kahlenberg, & Wrangham, 2009; Wingfield, Jacobs, & Hillgarth, 1997). The balance between cost and benefits of high levels of testosterone is at the foundation of the “challenge hypothesis” (Wingfield, Hegner, Dufty Jr, & Ball, 1990). Originally developed in birds, the challenge hypothesis predicts that testosterone levels only increase during periods of social instability when males are being challenged by other males for access to mates (Wingfield et al., 1990). The challenge hypothesis is supported by broad evidence in primates.

In species where males aggressively compete for access to females in mating contexts, testosterone increases during mating periods in both seasonally and non-seasonally breeding species (e.g., ring-tailed lemurs, *Lemur catta*: Gould & Ziegler, 2007; golden lion tamarins, *Leontopithecus rosalia*: Bales, French, McWilliams, Lake, & Dietz, 2006; rhesus macaques, Higham, Heistermann, & Maestripieri, 2013; chimpanzees, *Pan troglodytes*: Sobolewski, Brown, & Mitani, 2013; reviewed in Muller, 2017). In species where male reproductive competition is less related to mating contexts, no relationship has been found between testosterone and mating period (e.g., tufted capuchins, *Cebus paella*: Lynch, Ziegler, & Strier, 2002; muriquis, *Brachyteles arachnoides*: Strier, Ziegler, & Wittwer, 1999; moustached tamarins, *Saguinus mystax*: Huck, Löttker, Heymann, & Heistermann, 2005). However, in species with one-male group structure or species where the alpha male successfully monopolizes reproduction, testosterone levels were found to correlate with dominance rank and aggressive behaviors during periods when the social stability of the group was disrupted (e.g. mantled howler monkeys, *Alouatta palliata*: Cristóbal-Azkarate, Chavira, Boeck, Rodríguez-Luna, & Veàl, 2006; ursine colobus monkeys, *Colobus velerosus*: Teichroeb & Sicotte, 2008; chacma baboons, *Papio hamadryas*: Beehner, Bergman, Cheney, Seyfarth, & Whitten, 2006; siamangs, *Symphalangus syndactylus*: Morino, 2015; reviewed in Higham, Heistermann, et al., 2013; Muller, 2017).

In contrast, when the male dominance hierarchy was stable, testosterone levels did not correlate with dominance rank and aggressive behaviors (e.g., olive baboons, *P. anubis*: Sapolsky, 1993; Verreaux sifakas, *Propithecus verreaux*: Brockman, Whitten, Richard, & Benander, 2001; bearded capuchins, *Sapajus libidinosus*: Mendonca-Furtado et al., 2014, reviewed in Muller, 2017). Lastly, in species where dominance rank predicts mating access, testosterone levels were correlated with dominance rank (e.g., gray-cheeked mangabeys, *Lophocebus albigena*, Arlet et al., 2011; white-faced capuchins, *Cebus capucinus*, Schoof et al., 2016; mandrills, *M. sphin*x, Setchell et al., 2008; orangutans, *Pongo pygmaeus*, Marty et al., 2015; reviewed in Muller, 2017). However, inconsistency in the relationships between testosterone and dominance rank remains, and factors to explain such variation are still unclear (reviewed in Klinkova, Heistermann, & Hodges, 2004; Muller, 2017).

In northern pig-tailed macaques (*M. leonina*), both males and females exhibit red coloration in their face, genitalia, and rump. Males display a red line extending from the outer corner of their eye. They also develop a red patch of variable form around the anus, with a continuous red line reaching the penis by passing in-between the ischial callosities and over the scrotum (Figure 6.1). The adaptive function of this conspicuous signal has not been studied. Northern pig-tailed macaques live in multi-male, multi-female groups with a female-biased adult sex ratio. The species is characterized by considerable sexual dimorphism in canine size and body weight (male weight: 8.9±0.4 kg, *n*=2; female weight: 5.1±0.6 kg, *n*=11; Malaivijitnond et al., 2012; Smith & Jungers, 1997) and a strong male dominance hierarchy (Carlson, 2011). This suggests that male-male competition plays an important role in driving social relationships among males and between males and females. In Chapter 4, behavioral data and genetic paternity analyses indicated a significant relationship between mating success and dominance rank among resident males, with the alpha male siring most of, but not all, the offspring. Furthermore, when approaching other conspecific males or receptive females, males would often raise the tail, to display the conspicuous anoscrotal color to other individuals (pers. obs.), suggesting that the male red coloration may be used to signal male dominance rank as a badge of status. At the same time the red coloration is also shown to females, suggesting that this signal could also be used to attract females.

Indeed, female mate choice could be an alternative explanation of the adaptive function of the male ornament in northern pig-tailed macaque, as observed in rhesus macaque (Dubuc, Allen, et al., 2014). Based on the results from Chapter 4, receptive females overlap and copulate with multiple males during period of mating activity. I also found that dominance rank is not consistently a reliable predictor of mating and reproductive success, with great variation of observed mating and reproductive success between the two alpha males. Furthermore, receptive females were observed leaving the group temporarily or travelling at the periphery of the group to approach and copulate with subordinate males or EGMs (see Chapter 5). Confirmed paternity was reported for two middle-ranking males, including a subadult, and EGMs (see Chapter 4). Consequently, the diversity of female mating partners suggests that the male red signal could be used by females for mate choice.

In this chapter, I investigated the relationships between male sexual skin color, dominance rank, sociosexual behavior, and testosterone in one group of wild northern pig-tailed macaques (CH group) at Khao National Park, Thailand. I tested the following two non-mutually exclusive hypotheses and predictions: 1) male coloration is used as a badge of status (H_1), such that darker red male have a higher dominance rank (P_{1a}); and 2) male coloration is attractive to females (H_2), such that darker red males, independent of their dominance rank, have more mating partners (P_{2a}), have higher reproductive success (estimated via mating success) (P_{2b}), receive more female proceptive behaviors (P_{2c}), receive more female receptive behaviors (P_{2d}), consort more with receptive females (P_{2e}), and groom more with receptive females (P_{2f}). In regards to the relationships with male testosterone levels and following the challenge hypothesis, I considered that testosterone levels change with the degree of male competition for access to mates (H_3). For this hypothesis, I predicted that male testosterone levels would positively correlate with male dominance rank during periods of social instability (change of dominance rank) (P_{3a}) and would increase during female mating activity when male mating competition increases with the presence of EGMs and the number of receptive females (P_{3b}). Finally, if the red coloration is only used as a badge of status (H_1), I predicted that male red coloration should be an honest signal of their current androgen status and competitive ability with a positive correlation between testosterone levels and the intensity of red male coloration (P_{1b}).

To test these hypotheses, I collected digital images of male anogenital area to quantitatively and objectively measure the red coloration, fecal samples from males for the measurement of testosterone levels by enzyme immunoassays, and behavioral data on male dominance rank and female behaviors over a 13-month period. Male reproductive success was estimated via observed mating success, instead of genetic paternity data, because the number of infants on which paternity testing was conducted was very limited for the analysis of this chapter (see Chapter 4). Analyses were organized into four goals: 1) to investigate the association between male color and dominance rank (badge of status hypothesis); 2) to examine the relationships between male color, dominance rank, mating success, male-female association, and female behaviors towards males (female mate choice hypothesis); 3) to assess the association between testosterone levels and male dominance rank, and social instability; and 4) to test for a relationship between testosterone levels and mating activity.

6.B. Methods

6.B.1. Study site and subjects

The study site is located in the Mo Singto area in KYNP, northeastern Thailand (2,168 km^2; 14°26′42″ N, 101°21′56″ E; 130 km NE of Bangkok). The larger Mo Singto area is around 10 km^2 (José-Domínguez, Huynen, et al., 2015; Reichard et al., 2012) and is covered by a seasonal tropical forest, with an altitudinal range of 730-890 m above sea level (Kitamura et al., 2005; Kitamura et al., 2008; Reichard et al., 2012; Smitinand, 1989). KYNP can be characterized by a rainy season (May-Oct.), a cold season (Nov.-Feb.), and a hot season (Mar.-Apr) (for further details, see 2.C. Study Site).

For this chapter, systematic data collection occured from Sep. 2015-Nov. 2016 on CH group, which was entirely wild-feeding (José-Domínguez, Huynen, et al., 2015; José-Domínguez, Savini, et al., 2015). I divided the study into two phases: Phase I—a two-month period (Sep.-Oct. 2015)—was used to identify all subadult and adult individuals of the group. Phase II—a 13-month period (Nov. 2015-2016)—was the main behavioral and morphological data collection period (for further details, see 2.E.1. Timeline for Data Collection). From Sep. 2015-Nov. 2016, CH group was composed of 6-10 resident males (3-5 adult males and 3-6 subadult males), 18-24 adult females, and an estimated 35-45 immature individuals (see Figure 3.1).

6.B.2. Behavioral data collection

One to three observers (CC-B, CB, MR, NL, and/or FT) recorded behavioral data during females' receptive periods throughout Study Phase II (four to six days a week, 7 am-6 pm; for further details, see 2.E.3. Behavioral Data Collection). From Aug.-Nov. 2016, only FT collected data. Continuous focal sampling (focal sampling) (Altmann, 1974; Martin & Bateson, 2007) were collected for 14 receptive periods (5 in 2015, 9 in 2016) of 14 females (3 nulliparous, 11 parous), at one- to three-day intervals with a total of 104.2 hours in 2015 and 454.6 hours in 2016 (for further details, including definition of female's receptive period, see 4.B.2. Behavioral Data Collection). In addition, *ad-libitum* data (Altmann, 1974; Martin & Bateson, 2007) provided information on 12 receptive periods (8 in 2015, 4 in 2016) of 10 parous females. Focal sampling was also conducted on males (four adults, one subadult) every one to three days with a total of 59.5 hours in 2015 and 42.3 hours in 2016 (see Table 4.2) between Nov. 2015-Mar. 2016. From April 2016 until the end of the study, males could not be followed during the mating period as more than two females were simultaneously receptive and only these females were observed. During focal follows, all behavioral data were recorded on an iPad mini 4 using the Animal Behavior Pro iOS App (Newton-Fisher, 2012). Using a random number generator, focal individuals were chosen randomly to achieve an unbiased, equal daily observation time for each focal animal.

During focal follows, copulations and ejaculatory copulations (Table 6.1) and the identity of the focal individual’s partner were recorded. To assess female attraction to males, I recorded the occurrence of female proceptive behaviors: 1) presentation; 2) look back, lip-smack, kiss, and reach back during copulation; and 3) copulation calls following copulation (Table 6.1). To assess acceptance of a male by the female, I recorded female receptive behaviors based on the occurrence of: 1) female positive reaction to 1a) male approach (i.e., lip-smack, excited grunt) and 1b) male proceptive behavior (i.e., lip-smack, excited grunt); and 2) female negative reaction to 2a) male approach (i.e., avoid, flee, squeak), 2b) male proceptive behavior (i.e., flee), and 2c) male attempt to inspect/mount female (i.e., sit down, crouch submission, flee) (Table 6.1). As a female’s negative reaction to male behaviors, I also noted instances when the female interrupted consortship (i.e., walk or run away from the male) and copulation (i.e., squeak, crouch submission, run away) (Table 6.1). I also recorded consortship between a male and a receptive female and the occurrence of grooming between those two same partners (Table 6.1).

Overall, female behavioral data were analyzed as follows (Table 6.1):

1) Mating activity: number of receptive females, number of mating partners per male, rate of

copulation, and rate of ejaculatory copulation (the latter two calculated separately, as N per focal hour per month).

2) Percentage of proceptive behaviors (as percentage of the total number of mounts per month) with presentation and copulation call calculated separately, and the rest of proceptive behaviors during copulation combined together (as average of percentage of the total number of mounts per month).

3) Rate of receptive behaviors: positive female reaction to male combined together (as average N per focal hour per month), negative reaction to male with the percentage of consortship and copulation interrupted by female calculated separately (as percentage of total number of consort and total number of mounts per month, respectively) and other negative female reactions combined together (as average N per focal hour per month).

4) Time spent in consortship (as percentage of focal time per month).

5) Percentage of grooming occurrence after copulation (as N per focal hour per month) and time spent in grooming (as percentage of focal time per month).

6.B.3. Male dominance rank

The male dominance hierarchy was established from all dyadic interactions of aggression and submission between two males. Bidirectional agonistic behaviors, in which two individuals aggressed each other, were not included in this analysis. Only subadult males, who engaged in agonistic interactions with adult males and copulated with receptive females, were included in the male dominance hierarchy. Immigrant males and EGMs interacted rarely with the resident males, therefore they could not be included in the dominance hierarchy. The corrected, normalized David’s scores was used to assess dominance rank (de Vries et al., 2006), using the package “steepness” (Leiva & de Vries, 2014) in R v. 3.5.1 statistical software package (R Development Core Team, 2018) based on a sociometric matrix of wins calculated for each dyad (see also 3.B.3. Dominance Hierarchy). Male dominance hierarchy was divided into three categories: high-ranking males (alpha and beta males), middle-ranking males (ranks 3-4), and low-ranking males (ranks 5-9).

I witnessed two male take-overs of the alpha male position, each by an immigrant male (see 3.C.3. Take-overs of Male Dominance). With three-to-four adult males resident in the group at any time, the first seven months (Sep. 2015-Mar. 2016) had adult male dominance rank Ting-Snoopy-Kanhuh, briefly interrupted by approximately one week of instability when Farang took over the alpha male position (male change Ting-Farang). In April 2016, the dominance rank changed (male change Ting-Khao) and re-stabilized as Khao-Snoopy-Ting-Kanhuh for the remaining eight months (Apr.-Nov. 2016). In the data analysis, period of social instability were defined as followed (adapted from Setchell et al., 2008). A month was defined as “stable” when no changes in alpha male position occurred, while a month was defined as “unstable” when a change in alpha male position occurred.

6.B.4. Male androgen analysis

6.B.4.a. Fecal sampling. Between Nov. 2015-2016, a total of 131 fecal samples were collected from nine adult males: all four resident adult males (Ting, Khao, Snoopy, and Kanhuh) regularly observed in the group, one adult male (Farang) who was only observed in November and December 2015, and four EGMs (Chuan, Drogo, Mii, Ram) that were observed occasionally between Feb.-Oct. 2016 (see Figure 3.1). Among resident males, a mean of 2.2±0.6 samples were collected per month with a mean of 28.8±7.2 samples per male. For the rest of the males, six fecal samples were collected for Farang during the period that he took over the alpha male position, seven for Mii from Feb.-Mar. 2016, and one each for Chuan, Drogo, and Ram in February, July and September 2016, respectively. Fecal samples were collected immediately after defecation between 7 am-6 pm. The fecal samples were kept in a cooler containing ice packs while in the field, and then kept frozen at -80˚C until extraction.

6.B.4.b. Androgen extraction. Fecal samples were extracted following the method of Brown and colleagues (2005) at the Laboratory of Hormonal Analysis, Khao Khew Open Zoo, Thailand. Fecal samples were homogenized and dried in an oven at 60˚C. A portion of 0.2 g of dry feces was selected, resuspended in 5 ml of 90% ethanol, and vortexed briefly. The suspension was boiled into a water bath at 96˚C for 20 min (while keeping the level of ethanol to pre-boil level) and then centrifuged at 3,500 rpm for 20 min. The supernatant was transferred into a new tube. The original tube containing the fecal pellet was resuspended in 5 ml of 90% ethanol, vortexed for 30 s, and centrifuge at 3,500 rpm for 15 min. The supernatant was transferred to the tube containing the first supernatant and dried down under air in a warm water bath. The supernatant was resuspended in 1 ml of methanol, vortexed for 15 s, dried down again, resuspended again in 1 ml of methanol, and vortexed for 30 s. The extract samples were stored at -20˚C. Extraction efficiency was estimated by assessing the recovery of 3H-testosterone (3,000 counts per min) and mean extraction efficiency was >80%.

6.B.4.c. Immunoassay. Microtitreplate enzyme immunoassay (EIA) was used to analyze fecal extracts for immunoreactive testosterone, using a testosterone horseradish peroxidase (HRP) conjugated label (C. Munro, UC Davis, USA) and following the method of Brown and colleagues (2005). The EIA analysis was conducted at the laboratory of hormonal analysis, Khao Khew Open Zoo, Thailand. The immunoreactive testosterone includes multiple immunoreactive elements with native testosterone expected to be a minor component and was noted as fecal immunoreactive testosterone (fecal iT) (Setchell et al., 2008).

For all assays, standards, controls, and fecal extract samples were diluted in enzyme immunoassay buffer (A2 buffer, 1x working solution, pH 7.5). The 5x A2 buffer contained 0.5% of Tween® 20, 68.4 mM of Trizma® Base, 430 mM of Trizma® HCl, 750 mM of NaCl, 50 mM of EDTA, 0.45 % of Kathon® CG/ICP, and 5 mg/ml of BSA pH 7.0. Fecal extracts were diluted 1:250 in A2 assay buffer. Standards in doubling dilution were diluted by mixing 200 µl of standard stocks and 200 µl of A2 assay buffer (standard value range 2.34–600 pg/well). Testosterone-HRP was diluted 1:45,000 in A2 assay buffer. Testosterone antibody (R156/7, U.C. Davis) was diluted 1:55,000 in A2 assay buffer. For all assays, 50 µl of standards, controls, and fecal extract samples were added in duplicate to each well of a pre-coated goat-anti rabbit IgG plate (SCBI, EndoLab®). Immediately after, 25 µl of diluted testosterone-HRP and 25 µl of diluted antibody were added to each well of the plate. The plates were covered and incubated on shaker at room temperature for 2 hours. Following incubation of the plates, the plates were washed four times with wash solution, blotted dry, and then incubated with 100 µl of moss TMB for 7-10 min in the dark at room temperature, after which 50 µl of STOP solution (1N HCL) was added to each well. Absorbance was measured at 450 nm (reference 630 nm) on a plate reader.

A quality control was conducted to validate the laboratory assay by checking parallelism, recovery/accuracy, and sensitivity. Serial dilutions of fecal extracts from different males gave displacement curves parallel to those obtained for the testosterone standard for 20-90% binding.

All samples were analyzed in duplicate and the assay sensitivity was 0.05 ng/ml (88% binding). For the EIA, the intra- and inter-assay coefficients of variation of high- and low-value quality controls of testosterone were 3.49% and 4.53% (high) and 4.87% and 2.46% (low), respectively. Fecal iT levels were expressed as microgram of hormone per gram of dry feces.

6.B.5. Assessment of male skin color and luminance

6.B.5.a. Collection of digital color images. Hindquarter images were collected non-invasively from seven adult males for whom fecal iT levels were assessed, including four resident adult males (Ting, Khao, Snoopy, and Kanhuh) and three immigrant adult males/EGMs (Farang, Mii, and Ram) (see 6.B.4.a. Fecal Sampling). Skin color images were collected from Oct. 2015-Nov. 2016, including the two mating peaks (see Chapter 3 and Figure 3.1).

Digital images of male subjects and a color standard (X-rite ColorChecker passport) were taken following the "sequential method", a method described and validated in previous studies (Bergman & Beehner, 2008; Dubuc, Allen, et al., 2014; Higham, 2006; Higham, Pfefferle, et al., 2013; Stevens et al., 2009). A first digital image of male's hindquarters was taken from 1-6 m away from subjects (Figure 6.2) and captured in RAW format using a Nikon D3300 with an AF-S DX Nikkor with a 24.2-megapixels CMOS DX-format sensor and an AF-S DX Nikkor 55-200 mm f/4-5.6 ED VR II lens in manual mode. Immediately after the capture of a subject's image, a second image of the color standard was taken in the same location of the subject (Figure 6.2) to standardize images for ambient light and camera settings (Bergman & Beehner, 2008; Dubuc, Allen, et al., 2014; Higham, 2006; Higham, Pfefferle, et al., 2013; Stevens et al., 2009). Multiple series of images were taken for the four resident males during the study period (mean±SD, 21±8.5 images per male, range 9-29) with 1.9±0.8 images per month and per male (range, 0-7). In September 2016, no image could be collected. For the three other males, Farang, Ram, Mii, five, one, and three images were taken in December 2015, February 2016, and March 2016, respectively.

6.B.5.b. Standardization of digital images and area selection for measurement. Skin coloration was computationally quantified using the Image Calibration and Analysis Toolbox (micaToolbox version 1.22 Windows, Troscianko & Stevens, 2015) for the free open source ImageJ 1.52h software (Schneider, Rasband, & Eliceiri, 2012) to objectively measure and compare skin coloration (Troscianko & Stevens, 2015). I followed the method described in detail by Troscianko and Stevens (2015) and which has previously been used and validated in different animal species (Marshall, Philpot, & Stevens, 2015; Russell & Dierssen, 2015; Stevens et al., 2015; Troscianko, Wilson-Aggarwal, Stevens, & Spottiswoode, 2016).

The RAW images of the subject and color standard were transferred to the software using DCRAW (Coffin, 2015) to open RAW files in a linear fashion (Chakrabarti, Scharstein, & Zickler, 2009). For each image, a “multispectral image” (i.e., a stack of images with red, green, and blue channels; Troscianko & Stevens, 2015) was created and saved as “.mspec files”. The multispectral stack was then converted to 32-bits per channel and normalized using the grey patches from the color standard with standard reflectance values. The normalization process standardizes images for ambient light and camera settings. Using the polygon tool, a region of interest (ROI) below the male’s anus was selected to specify the region of the male skin area that will be used for measurement (Figure 6.2). This region was selected because the color was relatively uniform and it minimizes the effect of any local variation that may affect color measurements, such as sunlight, shadows, or decreased visibility from the tail or fur. The mean reflectance of each channel was then calculated in the ROI.

6.B.5.c. Generating cone mapping model. The ROI was converted from the camera color space to the macaque color space (cone-catch values) by generating a cone mapping model. This process requires defining the camera spectral sensitivities and macaque photoreceptor sensitivities. The mapping from the camera color space to the macaque color space is performed by simulating the camera photoreceptor responses and macaque predicted photoreceptor responses to a set of natural spectra that encompasses the natural range of the signal being estimated—all under D65 lighting conditions.

To map from the camera to the macaque color space, I used natural spectra samples of red-pink coloration from human skin spectra (data from NCSU spectral database) and from non-human skin spectra: long-tailed macaques (*Macaca fascicularis*), red uakaris (*Cacajao rubicundus*), and mandrills (*M. sphinx*) (data taken from http://vision.psychol.cam.ac.uk/spectra/). As I was unable to obtain the camera spectral sensitivity data for the camera model Nikon D3300 used to take images, I used data from a similar model camera, the Nikon D5200 (Jiang, Liu, Gu, & Süsstrunk, 2013) (Figure 6.3). The error associated with using the Nikon D5200 data instead of the Nikon D3300 should be negligible. Likewise, I was unable to obtain data on the spectral sensitivity of northern pig-tailed macaque longwave (LW), mediumwave (MW), and shortwave (SW) cones in response to the colors, so I used data from the rhesus macaque for MW and LW cones (data from Bowmaker, Dartnall, Lythgoe, & Mollon, 1978) and from humans for SW cone (data from Dartnall, Bowmaker, & Mollon, 1983) (Figure 6.4). The error associated with these differences should be negligible because: 1) the photoreceptors of the LW and MW cones are very similar to that of other macaque species (Packer, Hendrickson, & Curcio, 1989); and 2) the SW cone sensitivity shows little variation between trichromatic primates, and the signal, being red (and not blue), does not reflect significantly at short wavelengths (see Higham et al., 2010).

A polynomial color space transformation was then generated that can calculate macaque photoreceptor cone-catch values from camera photoreceptor values (Troscianko & Stevens, 2015). For each ROI, a mean of receptor cone-catch values was calculated in each channel (LW, MW, and SW). These data were used for comparing color and luminance (see below).

<u>6.B.5.d. Modeling color and luminance for pairwise discriminant comparison.</u> Skin reflectance modulation is determined by two blood-related dimensions: 1) skin color (redness) reflects blood oxygenation, such that redder skin contains more oxygenated haemoglobin; and 2) skin luminance (darkness) reflects blood flow, such that darker skin (less luminous) possesses greater haemoglobin concentration in the skin (Changizi et al., 2006; Zonios et al., 2001). Both of these parameters were estimated to assess variation in male anogenital skin reflectance.

I used the Vorobyev-Osorio receptor noise model (Vorobyev & Osorio, 1998), which calculates “just noticeable difference” (JND) values. This method is commonly used for comparing color and luminance in non-human visual systems to assess whether two similar signals are likely to be discriminable to the macaque visual system (Siddiqi et al., 2004; Troscianko & Stevens, 2015; Vorobyev & Osorio, 1998). The model is based on the relative cone abundance of the different photoreceptor types and estimate signal-to-noise ratios for each cone type that limits the discrimination of two signals (Higham et al., 2010; Vorobyev & Osorio, 1998). For color, I used relative cone abundance values in the proportion of 1:16:16 (see Higham et al., 2010) and global Weber fraction values of 0.08 for the SW cones and 0.02 for both the MW and the LW cones (Osorio, Smith, Vorobyev, & Buchanan-Smith, 2004; Osorio & Vorobyev, 1996; see Higham et al., 2010). For luminance, I used a global Weber fraction of 0.08 (Higham et al., 2010; Osorio & Vorobyev, 2005).

The Vorobyev-Osorio receptor noise model produces only relative values to compare two signals and one signal cannot be assessed independently (Higham et al., 2010). Consequently, the color and luminance of each ROI need to be compared to other ROIs. I followed the method described by Higham and colleagues (2010). For intraindividual analyses, I selected for each male the ROI with the lightest coloration (lowest color and highest luminance) and compared all other ROIs to this ROI. For interindividual analyses, I selected across all males the ROI with the lightest coloration and compared all other ROIs to this ROI. By doing so, positive JND values of color and luminance represent increasing intensity of redness and darkness, respectively. In the model, JND values less than one indicate that two signals are indistinguishable. JND values between one and three indicate that two signals are discriminable in good light conditions. Above three JNDs, the higher the value, the more discriminable the two signals are, even under deteriorated light conditions (Siddiqi et al., 2004).

6.B.6. Statistical analysis

I used generalized linear mixed models (GLMMs) to assess: 1) the effect of sexual skin color and luminance (fixed effects) on female behaviors towards males (proceptive and receptive behaviors), grooming, and consortship (response variables) while holding constant for male dominance rank (fixed effect); 2) the effect of sexual skin color and luminance (fixed effects) on mating success (copulation and ejaculatory copulation, separately) and the number of mating partners (response variables) while holding for male dominance rank (fixed effect); and 3) the effect of the number of receptive females (fixed effect) on sexual skin color and luminance (response variables). In all GLMMs, male ID was added as a random effect to control for multiple observation on the same date and of the same individual. For these GLMMs, I also looked at both main mating periods separately (period 1: October-December 2015, period 2: June-November 2016) because of the change in alpha male in April 2016 (rank change Ting-Khao) and temporal variation of male skin coloration.

I also used generalized linear mixed models (GLMMs) to examine the effect of fecal iT and dominance rank (fixed effects) on sexual skin coloration (color and luminance; response variables), while holding for dominance rank (random factor). I also ran these GLMMs in both periods before and after the rank change Ting-Khao. Color and luminance measures were not available for every day that a fecal testosterone level was assessed. Therefore, fecal iT's were compared for each male with the closest day they had color and luminance measured (mean=0.6 days between fecal sample and image sample, range: 0-3 days). Finally, I used GLMMs to investigate the relationships between dominance rank (response variable) and fecal iT (fixed effect) and the effect of rank instability (fixed effect) on fecal iT (response variable), with male ID as a random factor.

All statistical tests were calculated with the R v. 3.5.1 statistical software (R Development Core Team 2018). The library "lmerTest" (Kuznetsova, B., & H.B., 2017) was used for GLMMs.

6.C. Results

6.C.1. Intra- and interindividual perceptual variation of male coloration

Visual modeling of male anogenital skin coloration showed discriminable perceptual variation in color (redness) and luminance (darkness) between males, which fluctuated over time throughout the study period (Table 6.2, Figures 6.5 and 6.6). Intraindividual difference of color and luminance varied from as little as 0.4 and 0.2 JNDs to as much as 39.3 and 17.2 JNDs from their own individual maximum value, respectively. Interindividual difference of color and luminance varied from as little as 1.1 and 0.7 JNDs to as much as 43.0 and 18.2 JNDs from all the male maxima. While color and luminance both showed perceptible variation to the macaque visual system, color variation was higher (i.e., more perceptible) than luminance.

6.C.2. Male coloration, dominance rank, and mating success

The GLMMs revealed that dominance rank did not influence male skin color (Figure 6.5) and luminance (all $p>0.1$; Table 6.3, Figure 6.6). However, a difference of male color profiles could be observed before and after the rank change Ting-Khao. Before the rank change Ting-Khao, male color was not correlated with dominance rank ($p>0.1$), such that the beta and third-ranking males had redder color than the alpha male (>4 JNDs). However, after the rank change Ting-Khao, male color and dominance rank were significantly negatively correlated ($t=-5.014$, $n=22$, $p<0.001$), such that the alpha male had the reddest color, closely followed by the beta male (<4 JNDs). This difference of patterns before and after the rank change Ting-Khao could also be observed with luminance, but to a lesser degree. Before the rank change Ting-Khao, no correlation was found between male dominance rank and luminance ($p>0.1$). After the rank change Ting-Khao, dominance rank and luminance were significantly negatively correlated (t=-3.616, n=22, p=0.003), with a luminance between the alpha male and the beta male less than 4 JNDs most of the time.

Farang, who took over the alpha male position for less than 10 days in December 2015, was darker and redder than any other resident male (at least >5 JNDs and >3 JNDs, respectively). The two EGMs (Mii and Ram) showed relatively high levels of redness and darkness, similar to the beta male. Because of the limited data set for EGMs, they could not be included in the statistical analysis.

To summarize, these results showed contrasting evidence to support the prediction that darker red males have higher dominance rank (P_{1a}), and consequently, to support the hypothesis that male skin color may be used as a badge of status (H_1).

6.C.3. Male coloration, receptive females, mating success, and female behaviors

The monthly number of receptive females was 3.0±1.9 during the mating periods (range, 1-6). The GLMM revealed that male color and luminance was significantly positively correlated with the number of receptive females (color: t=2.416, n=37, p=0.041, luminance: t=2.534, n=37, p=0.033; Table 6.3). The redness and darkness of skin color perceptibly increased among the four resident males during the mating periods with greater interindividual differences (Figures 6.5 and 6.6). During mating period 1, the beta male exhibited the darkest and reddest skin coloration, while the alpha male was the lightest and least red male. In contrast, both the alpha male and beta male exhibited the reddest and darkest skin coloration during the mating period 2, especially during the month of higher mating activity (high number of receptive females). The lowest-ranking male showed the lowest increase in redness and darkness, but still perceptible by the females (>5 JNDs) between period of mating and non-mating activity.

Resident males had 1.5±1.1 (mean±SEM) mating partners per month (range, 0-3). The GLMMs showed that male skin color and luminance were significantly positively correlated with the number of mating partners during the study period (color: t=2.464, n=25, p<0.022, luminance: t=3.423, n=25, p=0.003; Table 6.4) and for each mating period (mating period 1: color: t=19.765, n=5, p=0.032, luminance: t=6.664, n=5, p=0.022; mating period 2: color: t=5.122, n=14, p<0.001, luminance: t=6.240, n=14, p=0.003; Table 6.4), such that darker and redder males had more mating partners. These results supported my prediction (P_{2a}).

Resident males were involved in 7.5±4.9 copulations and ejaculatory copulations (range, 1-19), and spent 18.6±19.1% of the observation time in consortships per month during the mating periods (range, 0-88%). There was no significant correlation found between male mating success (rate of copulation and rate of ejaculatory copulations, separately) and skin color and luminance during the study period and for each mating period (all p>0.1; Table 6.4). These results rejected my prediction (P_{2b}).

In regards to female proceptive behaviors, females presented in 28.9±24.2% of the mounts (range, 0-78.6%) and gave copulation calls in 18.9±24.4% of the mounts (range, 0-92.9%) during the mating periods. The GLMMs showed that male skin color and luminance significantly affected female proceptive behaviors (i.e., look back, kiss, lip-smack, reach back) during the entire study period (color: t=2.061, n=25, p=0.050, luminance: t=2.265, n=25, p=0.050; Table 6.4) and mating period 1 (color: t=12.39, n=5, p=0.050, luminance: t=-12.51, n=5, p=0.050; Table 6.4), with females performing more proceptive behaviors with darker red males during copulations. Such significant correlation was not found during the mating period 2 (p>0.1). No effect of male skin coloration was found on female presentation and copulation calls during any periods (all $p>0.1$; Table 6.4). However, male skin color and luminance significantly affected copulation calls during mating period 1 (color: $t=-2.553$, $n=14$, $p=0.029$, luminance: $t=2.828$, $n=14$, $p=0.018$; Table 6.4), with receptive females giving more copulation calls after a mount with a darker and redder male. Thus, taken altogether, these results partially supported my prediction (P_{2c}) that females tended to perform more proceptive behaviors with darker red males during copulations.

As for female receptive behaviors, females interrupted 9.6±20.3% of the mounts (range, 0-100%) and 14.9±20.9% of the consorts (range, 0-37.5%) during the mating periods. The GLMMs revealed that male skin color and luminance did not affect any female receptive behaviors (all $p>0.1$; Table 6.4), which rejected my prediction (P_{2d}). Male skin color and luminance significantly influenced consortship time with receptive females during mating period 1 (color: $t=260.4$, $n=5$, $p=0.001$, luminance: $t=-286.9$, $n=5$, $p=0.003$; Table 6.4), but not during the entire study period and mating period 2 (all $p>0.1$). These results showed contrasting evidence to support my prediction (P_{2e}).

Lastly, males and receptive females groomed 1.6±2.2% of the observation time (range, 0-8.9%) during mating periods. On average, 4.5±5.4% of the mount (range, 0-15.4%) was followed by a grooming session between the male and the receptive female during the mating periods. The GLMMs indicated that male skin color and luminance significantly positively influenced the occurrence of grooming after copulation during the entire study period (color: $t=3.391$, $n=25$, $p=0.003$, luminance: $t=3.478$, $n=25$, $p=0.002$) and during mating period 2 (color: $t=2.822$, $n=14$, $p=0.01$, luminance: $t=2.907$, $n=14$, $p=0.014$) and grooming duration during mating period 2 (color: $t=2.627$, $n=14$, $p=0.025$, luminance: $t=-2.238$, $n=14$, $p=0.049$; Table 6.4). However, no effect was found during mating period 1 (all $p > 0.1$). Thus, these results partially supported my predictions (P_{2f}).

To summarize, these results supported (at least partially) all my predictions that darker and redder males, independent of their dominance rank, had more mating partners (P_{2a}), received more proceptive behaviors (P_{2c}), consorted more with females (P_{2e}), and groomed more with receptive females (P_{2f}). However, darker and redder males did not have higher mating success (P_{2b}). Thus, these results suggest at some level that male colorful ornament is attractive to females (H_2).

6.C.4. Male coloration, dominance rank, and androgen

The GLMMs showed a significant negative correlation between dominance rank and fecal iT levels ($t=-4.128$, $n=34$, $p<0.001$; Table 6.5, Figure 6.7), but the coefficient of correlation was very close to zero (r=-0.002). A difference of fecal iT profiles could be observed before and after the rank change Ting-Khao. Dominance rank was significantly negatively correlated with fecal iT levels before the rank change Ting-Khao ($r=-0.839$, $t=-5.026$, $n=13$, $p<0.001$; Table 6.5), but not after the rank change Ting-Khao ($p>0.1$). The alpha male had a higher level of fecal iT before the change of rank (811.8±459.1 μg/g of dry feces, range, 86.3-1698.8) than the alpha male after the change of rank (319.4±157.5 μg/g of dry feces, range, 90.3-661.5). The latter alpha male Khao had fecal iT levels at a similar level to the beta male (406.0±253.3 μg/g of dry feces, range, 65.1-1066.1) or the former alpha male Ting (369.3±216.6 range, 18.0-833.6) after the rank change Ting-Khao. The beta male (410.2±211.0 μg/g of dry feces, range, 65.2-1066.1) and the lowest-ranking male (187.9±119.7 μg/g of dry feces, range, 84.2-614.0) showed relatively little variation of fecal iT levels throughout the study period.

There was no significant correlation between male fecal iT levels and color and luminance, and between fecal iT levels, social instability, and the number of receptive females (all *p*>0.1; Table 6.3 and 6.5). These results rejected my predictions (P_{3a}, P_{3b}, and P_{1b}) and do not support my hypothesis (H_3) that testosterone levels change with the degree of competition among the males for access to mates.

6.D. Discussion

Although red sexual skin is a conspicuous trait that occurs among a wide variety of male primates, the adaptive function of this ornament has so far only been meticulously investigated in four primate species: mandrills (Setchell, 2005; Setchell, 2016; Setchell & Dixson, 2001), drills (Marty et al., 2009), gelada baboons (Bergman & Beehner, 2008; Bergman et al., 2009), and rhesus macaque (Dubuc, Allen, et al., 2014; Dubuc, Winters, et al., 2014; Higham, Pfefferle, et al., 2013; Petersdorf et al., 2017). Further, among these studies, only few used a visual discrimination model (Higham, Pfefferle, et al., 2013). When studying primate color, it is important to prefer quantifying color methods that include the appropriate receiver's visual system, as the perception of color can greatly vary among human and non-human primates (Stevens et al., 2009). To our knowledge, this is the first study investigating the expression and function of male sexual skin coloration using a visual discrimination model in wild northern pig-tailed macaques.

The intensity of male sexual skin color fluctuated over time, such that males exhibited darker and redder skin color as the number of receptive females increased in the group. Darker and redder males had more mating partners and received more female proceptive behaviors during copulation. Male-female consortship was only significantly associated with male coloration during the mating period 1, while grooming duration only during the mating period 2. However, I found no evidence for a relationship between female receptive behavior and male sexual skin color. Overall, these results support the hypothesis that female northern pig-tailed macaques express, at some level, a preference for darker and redder males. There was contrasting evidence to support the relationships between male sexual skin color and dominance rank. While no significant correlation between male skin color and dominance rank over the entire study period was found, there was a significant correlation between male skin color and dominance rank after the change in alpha male, such that the alpha male and beta male had darker and redder skin. However, the alpha male before the change of rank had less and lighter red skin. Thus, results of this study may suggest that male colorful ornament, in addition to be attractive to females, may also act as a badge of status, though evidence for the latter function remained limited.

This study revealed that male sexual skin color did not influence male mating success. At first, this result might seem unexpected. Indeed, an ornament must influence reproductive success in order to demonstrate that it has been selected by intra- or intersexual selection (Snowdon, 2004), as demonstrated in mandrills (Setchell, 2005). It is possible that not all mating activity was captured as observed copulations may be non-representative of the actual mating success because of surreptitious mating that are more likely to be missed by observers (Alberts et al., 2006). For instance, at least three successful paternities by EGMs were reported in my study group while the female and the EGM who sired the offspring had not been seen copulating (see Chapter 4). Mating distribution may also be non-random if males invest more mating effort to females with higher fertility (Alberts et al., 2006). For instance, high-ranking males might exert mate choice towards multiparous females that are undergoing a conceptive cycle (rather than non-conceptive cycle) (Alberts et al., 2006).

Alternatively, mating success may not be a good predictor of reproductive success based on my results of the previous chapter (see Chapter 4) and a study in rhesus macaques (Dubuc et al., 2011). For instance, factors at the post-copulatory level could explain a mismatch between mating and reproductive success. When the dominant males cannot monopolize access to the females, female promiscuous copulation could lead to sperm competition within the female reproductive tract and affect conception success (Alberts et al., 2006; Birkhead & Hunter, 1990; Maestripieri & Roney, 2005). Furthermore, the lifetime reproductive success of males can remarkably vary from year to year in mammals with a slow-life history, such as the primates (Clutton-Brock, 1988; e.g., Alberts et al., 2006; Dubuc, Winters, et al., 2014). Therefore, male reproductive success measured over a one-year period is not necessarily a good reflection or representative example of an individual lifetime reproductive success.

Nonetheless, there is still the possibility that male skin color may not influence reproductive success and female attraction to such ornament could be a by-product of natural selection on sensory systems (Dubuc, Allen, et al., 2014; Endler & Basolo, 1998; Fuller, Houle, & Travis, 2005). The sensory bias hypothesis states that female mating preferences for specific male traits are by-products of the female sensory systems that were originally shaped through natural selection (and not through sexual selection), and that male traits evolved to match the female sensory systems (Endler & Basolo, 1998; Fuller et al., 2005). Only a long-term study with genetic paternity data from different social groups would help to understand whether male skin color influenced male reproductive success in northern pig-tailed macaques.

Despite this absence of correlation between male skin color and mating success, the results of this study support an attractive role of male skin color to females. Male skin color became redder and darker during the mating periods with an increase of intermale differences. In drills (Marty et al., 2009) and geladas (Bergman et al., 2009) in which male skin color acts solely as a badge of status, males maintain maximum level of color expression throughout the year. This need to maintain maximum color expression all year-round has been linked to the continuous high level of reproductive competition in those species and could explain the need to constantly signal competitive ability (Setchell & Dixson, 2001). In contrast, a temporal variation of male sexual skin color was observed in rhesus macaques (Baulu, 1976; Higham, Pfefferle, et al., 2013) and mandrills (Setchell et al., 2008). In rhesus macaques, males express darker and redder facial coloration to attract females but only during the mating season (Baulu, 1976; Higham, Pfefferle, et al., 2013). Interestingly, while male mandrills express bright coloration on their nose as a badge of status throughout the year (Setchell & Dixson, 2001), they also become brighter in the presence of receptive females (Setchell et al., 2008). Therefore, the temporal variation of male sexual skin color with the number of receptive females, as observed in the present study, supports the hypothesis that male color is used to attract females in northern pig-tailed macaques.

Northern pig-tailed macaques are characterized by a high degree of sexual dimorphism in body size and weight (Malaivijitnond et al., 2012) and a strong dominance hierarchy (see Chapter 3; Carlson, 2011). Consequently, male sexual skin color in this species should be expected to act as a badge of status to help resolve disputes without conflict, as in mandrills (Setchell & Dixson, 2001), drills (Marty et al., 2009), and geladas (Bergman et al., 2009). However, evidence for a dominance signal remained inconclusive in this study. During the entire study period, male skin color was not significantly linked to dominance rank but after the change in alpha male, it was. Such inconsistency seems odd, but a study in mandrills showed that alpha males do not necessarily exhibit the brightest red coloration despite a strong correlation between male red color and dominance rank (Setchell et al., 2008). Male mandrill ornament being most likely under both inter- and intraindividual selection, females may prefer a brighter red male that is not the alpha male (Setchell, 2005; Setchell et al., 2008). Alternatively, if indeed color signals status in my study group of northern pig-tailed macaques, the lighter and less red coloration displayed by the alpha male before he lost his top rank may indicate that the weaker signal corresponded to his already weaker status at the end of his alpha male tenure. Furthermore, the new alpha male Khao, who took over the dominance of the group, may already have had a darker and redder coloration than the resident males when he entered the group. Unfortunately, this idea cannot be evaluated in the absence of color measurement of Khao's sexual skin prior to the take-over. However, these interpretations conflict with observations in mandrills indicating that the loss/gain of dominance rank preceded the loss/gain of coloration, but not vice versa (Setchell et al., 2008).

In species where males exhibited red skin color as a badge of status, this signal is hypothesized to be used to decrease the cost of direct conflict (fights) between individuals that have limited social knowledge of their opponent. Indeed, mandrills and drills gather in "supergroups" of few hundreds individuals during the mating season (Gadsby, 1990; Rogers et al., 1996) and geladas and black-and-white snub-nosed monkeys live in multi-level societies that reach 300 individuals or more (Grueter, 2013; Kirkpatrick & Grueter, 2010; Snyder-Mackler, Beehner, & Bergman, 2012). In contrast, northern pig-tailed macaques live in stable to moderate sized groups of less than 100 individuals (see Chapter 3; Choudhury, 2008). Therefore, in their society, there may have been less selection pressure for evolution of a signal as a badge of status.

Still, data from a larger sample size including several social groups are needed to confirm this. Indeed, the small sample size of my study may have limited my ability to detect a significant correlation between male skin color and dominance rank.

Contrasting to findings in mandrills (Setchell et al., 2008), there was no significant correlation between male sex skin color (redness and darkness) and androgen levels. This result was unexpected as it has been previously shown that red skin color is controlled by testosterone in other primates (Rhodes et al., 1997). This odd result was also found in a study of rhesus macaques (Higham, Pfefferle, et al., 2013), where the authors suggested that sex skin-specific receptor expression could explain the results. In both mandrills (Setchell & Dixson, 2001; Setchell & Jean Wickings, 2005) and geladas (Bergman et al., 2009), males that become top-ranking subsequently develop more coloration, while deposed males lost coloration, but not vice versa. During a challenge, males display more aggressive behaviors (Bergman et al., 2009), which is most likely linked to an increase in androgen levels (Dixson, 2012; Setchell et al., 2008). Therefore, Higham and colleagues (2013) proposed that the sensitivity of sex skin-specific receptor expression may be lowered when androgen levels increase, even though the dominance rank may remain unaltered. Hence, androgen levels could vary without affecting male skin coloration. Similarly, it suggests that red skin color could be used as a reliable signal of male quality to females, independently of circulating androgen levels, in primate species where males exhibit red skin ornaments to attract females. Further experimental studies on tissue-specific receptor expression controlling red skin ornament are much needed as they may play an important role in primate signals (Higham, Pfefferle, et al., 2013).

This study found a significant relationship between dominance rank and androgens, but the coefficient of correlation was low (r=-0.002). When dividing the period before and after the change in alpha male, I found that before the change of rank, fecal iT was significantly linked to dominance rank with a higher negative coefficient of correlation (*r*=-0.839). The alpha male Ting had the highest level of testosterone despite being the lightest and least red male during this period. However, no correlation between fecal iT and male dominance rank was observed after the rank change Ting-Khao. The new alpha male Khao had fecal iT levels similar to the beta male Snoopy and former alpha male Ting during the same time period, but much lower than the former alpha male during the period prior to the rank change Ting-Khao. One possible explanation for this result was the ongoing social instability in the group. Even though I did not find an effect of the month with social instability, direct conflicts between the alpha male Ting and the contenders were observed in December 2015 (prior to and during the short-term takeover by Farang) and in April 2016 (when Khao challenged and disposed Ting; see 3.C.3. Take-overs of Male Dominance). Several of these fights resulted in serious injuries. After the rank change Ting-Khao in April 2016, no major conflict was observed among the resident males (pers. obs.). Thus, Ting may have faced higher levels of competition and aggressive behaviors between Nov.-Apr. 2016 than other resident males during that same period and Khao between Apr.-Nov. 2016. This could explain the higher level of fecal iT found in Ting than Khao. Such a potential effect of dominance instability (i.e., aggressive behaviors) on the relationships between dominance rank and androgens would be consistent with the challenge hypothesis (Muller, 2017). Multiple studies in rhesus macaques (Higham, Heistermann, et al., 2013), chacma baboons (Beehner et al., 2006), and olive baboons (Sapolsky, 1983, 1993) have confirmed such prediction in which dominance rank was only related to androgen levels during the period of social instability.

The absence of relationships between androgens and the number of receptive females suggests that male reproductive competition is less related to mating contexts despite the presence of EGMs during mating periods. Indeed, in species where male-male aggression is less important in mating context, no relationships has been found between testosterone and mating periods (Muller, 2017). In addition, the mixed results of the relationships between androgens and dominance rank found in this study reflect the inconsistent results observed among primates in general, with studies reporting a strong negative correlation, and others not (reviewed in Klinkova et al., 2004; Muller, 2017; Whitten, Brockman, & Stavisky, 1998). The reasons for such variation remain unclear as many factors could affect this relation. One reason might be that hormone-behavior relationships are more flexible than previously thought (Crews, 1984; Klinkova et al., 2004). Another possible reason has been related to the inconsistent definition of dominance itself and behaviors used to assess dominance hierarchies in the primate literature (Klinkova et al 2004). Lastly, the relationship between dominance rank and androgens may also depend on how individual rank-associated behaviors (e.g., aggressive behaviors, sexual behaviors) are affected by androgens in each species (Klinkova et al 2004).

Evidence to explain why females prefer darker red males and whether male red skin color is linked to male condition or quality in primates remains scarce and available for only few species. In rhesus macaques (Dubuc, Allen, et al., 2014) and mandrills (Setchell, 2005), red skin ornaments may be used as a honest signal of male quality by females. Indeed, red skin color is directly influenced by blood flow and oxygenation (Zonios et al., 2001, reviewed in Bradley & Mundy, 2008; Dixson, 2012), which can in turn be affected by physiological or environmental factors, such as stress, health, and social relationships (Bradley & Mundy, 2008; Dixson, 2012). Further, blood flow and oxygenation are reflected in the measurement of redness (color) and darkness (luminance) (Changizi et al., 2006; Stevens et al., 2009). These studies are consistent with a study from rhesus macaques (Dubuc, Allen, et al., 2014) where both intra- and interindividual variation of red coloration occurred in color and luminance. The authors of this study found that skin redness and darkness were found to be heritable traits that differently influence male and female fecundity (Dubuc, Winters, et al., 2014). This heritability was related to the underlying mechanism of the expression of such signal. Blood flow in red sex skin areas is controlled by testosterone concentrations and influenced by the number, sensitivity, and activation of estrogen-dependent receptors in these specific-skin areas (Rhodes et al., 1997). These receptors are under genetic control and most likely sex-influenced (Dubuc, Winters, et al., 2014). Thus, skin darkness (blood flow) in rhesus macaques is hypothesized to be more likely a condition-dependent signal under the influence of intersexual selection than skin redness (Dubuc, Winters, et al., 2014). In the present study, I found variation in redness and darkness of male skin color, which suggests that this male ornament could function as an honest signal that could be influenced by environmental and/or physiological factors. This remains to be confirmed in further studies of northern pig-tailed macaques and other primate species in which males exhibit red skin ornaments.

This study also faced some limitations. First, assessment of male sexual skin color could only be measured regularly from four resident males from one group. No systematic color measurement was possible for EGMs, despite confirmed paternity from those males (see Chapter 4). Second, all behavioral data for females were combined for each male due to the limited amount of data with the underlying assumption that females show uniform mating preferences. However, some females only copulated with dominant males, while others copulated with all resident males or only with subadult males and EGMs (see Chapter 5, pers. obs.). Variation of female mating preferences have been observed in primates (Dixson, 2012). For instance, females may prefer to copulate with males based on their genetic make-up (i.e., genetic compatibility;

Sauermann et al., 2001). Third, females' receptive periods were assessed from mating behaviors, but not from hormonal analyses to estimate the ovulation date and fertile period. A female may copulate promiscuously to confuse paternity and reduce the risk of infanticide, but may copulate with a preferred partner during her fertile period (Nunn, 1999a). Fourth, northern pig-tailed are semi-arboreal and live in dense tropical forest. Most copulations are recorded when individuals are on the ground and during daytime (pers. obs.). When individuals travel high up in the tree, near the canopy, observations of copulations become limited or impossible. Copulations can also happen early in the morning or late at night, when luminosity is too low to accurately record behaviors and identify individuals (pers. obs.).

In conclusion, this study revealed some evidence to support that male red skin ornament may be used as a signal to attract females in northern pig-tailed macaques. Mixed evidence was found to support the hypothesis that male red ornament acts as a badge of status. Further studies with a larger sample size of male color and long-term genetic paternity data are needed in northern pig-tailed macaques to investigate: 1) whether red skin ornament functions as an honest signal, a badge of status, or both at the same time; and 2) whether and to what extent male qualities are linked to this signal. Separating the effect of intersexual from intrasexual selection can be extremely difficult in primates because of: 1) their slow life history and slow reproductive rates leading to small data samples; and 2) the complex interaction of male and female reproductive strategies (Setchell, 2005; Setchell & Kappeler, 2003; Soltis et al., 2001; van Schaik et al., 2004). Thus, more detailed studies focusing on both mechanisms are much needed to better grasp the adaptive function of male ornaments in primates.

Lastly, while female northern pig-tailed macaques seemed to be attracted to darker and redder males, this does not rule out that females may actually prefer these males for other characteristics that I did not measure and that still need to be elucidated. The clear interindividual differences in size and patterns of the male red ornament could potentially affect female attraction. For instance, a male with a lighter red skin but over a larger surface area could be more conspicuous and attractive to females than a male with darker red skin but constrained to a smaller area. To clarify the relationship between color, shape, and size of the red sex skin in males, further studies are needed.

Table 6.1 Categories and definitions of mating activity and female-initiated behaviors of northern pig-tailed macaques and recorded in this study.

Female-initiated behaviors			**Definitions**	**Units**
Mating activity		*Mating partners of males*	A receptive female is a partner of a male when the receptive female and the male had at least one ejaculatory copulation	N/month
		Receptive females	A female was categorized as sexually receptive when she was seen mating (i.e. mounts, mounting series, evidence of sperm plug) (Dixson, 2012; Dubuc et al., 2012)	N/month
		Copulation	A series of one or more than one mount without ejaculation ending when the copulating pair is more than 10 m away from each other for more than 20 min and no ejaculation was observed (Manson, 1996; Overduin-de Vries et al., 2012; Soltis et al., 1999)	N/focal hour/month
		Ejaculatory copulation	A series of one or more than one mount ending by one ejaculatory mount (Manson, 1996; Overduin-de Vries et al., 2012; Soltis et al., 1999)	N/focal hour/month
Proceptive behaviors	Before copulation	*Presentation*	Stereotyped posture of a female raising or directing her perineum with hind legs rigid and extended toward a male (Eaton & Resko, 1974; Garcia et al., 2009; Goldfoot, 1971)	% of mount /month
	After copulation	*Copulation call*	Female utters rhythmic and low pitched vocalization after a mount (Maestripieri & Roney, 2005)	% of mount /month
	During copulation	*Look back*	The female gazes back at the male during mating (Bullock et al., 1972)	Avg. % of mount /month
		Kiss	The female brings her mouth close to the face or mouth of the male	
		Lip-smack	The female smack lips together	
		Reach back	The female reaches back to the hind leg of the male while the male mounts her (Bullock et al., 1972)	
Receptive behaviors: Reaction to male approach or male proceptive behaviors (pucker-thrust face, inspection, mount)	Positive	*Lip-smack*	The female smack lips together	Avg. N/focal hour/month
		Excited grunt	Female utters rhythmic and low pitched vocalization	
	Negative	*Consortship interrupted*	Female interrupts consortship by walking or running away from the male	% of consort /month
		Copulation interrupted	Female interrupts a mount by running away, submissive crouching, or squeaking	% of mount /month
		Avoid	One individual moves away ≥ 1 m (Setchell et al., 2005a)	Avg. N/focal hour/month
		Flee	One individual runs away ≥ 1 m (Setchell et al., 2005a)	
		Squeak	High-pitch vocalization by a female	
		Sit down	A female remains seated while a male is grasping her waist trying to inspect/mount her (Overduin-de Vries et al., 2012)	
		Crouch submission	A female lays down while a male start mounting the female leading to the interruption of copulation	
Consortship			A male and a female (1) are in persistent close proximity (< 10 m, one of them following the other), and (2) copulate during the day. A consort started when the male/female approached within 10 m and ended when either mated with another individual or when spatial proximity terminated (i.e., > 10 m apart) or one of the individuals ceased following the other for more than ten consecutive minutes. A consort was disrupted when a male and a female were forced to end their consort due to an interaction with another male (passive approach, agonistic behaviors) (Berard et al., 1994; Brauch et al., 2008)	% of focal hour/month
Grooming		*Groom*	One individual picking through a partner's skin or fur with one or both hands and transferring particles to its mouth (Eaton & Resko, 1974; Setchell et al., 2005a). A grooming bout ends after a 10-s pause in the behavior.	% of focal hour/month
		Groom after copulation	A male and a female groom each other after copulation	% of mount /month

Table 6.2 Intraindividual and interindividual maximum JND variation of male anogenital color and luminance. Values presented represent the average with SD maximum JND variation as well as the min and max JND scores among all males.

		$\bar{x}$	**SD**	**Min**	**Max**
Intra-individual variation (JNDs)	Color	5.0	5.3	0.4	39.3
	Luminance	6.9	4.3	0.2	17.2
Inter-individual variation (JNDs)	Color	6.8	5.7	1.1	43.0
	Luminance	7.9	4.2	0.7	18.2

Table 6.3 Results of GLMM's analyses to assess the relationship between male skin color and luminance, mating period (number of receptive females), dominance rank, and fecal iT. In all models, male dominance rank was added as a fixed effect and male ID as a random factor.

	Color	**Luminance**
Dominance rank	t=-0.713, n=37, p=0.488	t=1.148, n=37, p=0.260
No. of receptive females	t=2.416, n=37, p=0.041*	t=2.534, n=37, p=0.033*
Fecal iT	t=-0.259, n=57, p=0.796	t=1.338, n=57, p=0.187

*: $p \leq 0.05$.

Table 6.4 Results from GLMM's analyses to assess the influence of male skin color and luminance on mating success, female proceptive and receptive behaviors, consortship duration, and grooming.

			Mating period 1	**Mating period 2**	**Entire study period**
Mating success	Number of mating partners	*Color*	t=19.765, n=5, p=0.032*	t=5.122, n=14, p<0.001***	t=2.464, n=25, p=0.022*
		Luminance	t=6.664, n=5, p=0.022*	t=6.240, n=14, p=0.003**	t=3.423, n=25, p=0.003**
		Rank	t=-4.737, n=5, p=0.042*	t=1.722, n=14, p=0.221	t=-0.111, n=25, p=0.913
	Copulation	*Color*	t=1.297, n=5, p=0.418	t=2.009, n=14, p=0.072	t=--0.720, n=25, p=0.479
		Luminance	t=1.074, n=5, p=0.474	t=-1.403, n=14, p=0.191	t=1.003, n=25, p=0.327
		Rank	t=-1.868, n=5, p=0.294	t=2.216, n=14, p=0.106	t=-3.066, n=25, p=0.018*
	Ejaculatory copulation	*Color*	t=0.723, n=5, p=0.601	t=0.601, n=14, p=0.562	t=-0.942, n=25, p=0.357
		Luminance	t=0.555, n=5, p=0.676	t=-0.530, n=14, p=0.608	t=0.898, n=25, p=0.379
		Rank	t=-1.060, n=5, p=0.468	t=2.216, n=14, p=0.106	t=-2.431, n=25, p=0.038*
Female proceptive behaviors	Presentation	*Color*	t=-4.031, n=5, p=0.155	t=-0.794, n=14, p=0.446	t=0.289, n=25, p=0.775
		Luminance	t=-8.341, n=5, p=0.076	t=1.556, n=14, p=0.151	t=0.374, n=25, p=0.712
		Rank	t=-11.857, n=5, p=0.054	t=0.735, n=14, p=0.479	t=1.422, n=25, p=0.170
	Copulation call	*Color*	t=3.233, n=5, p=0.191	t=-2.553, n=14, p=0.029*	t=-0.543, n=25, p=0.593
		Luminance	t=-3.312, n=5, p=0.187	t=2.828, n=14, p=0.018*	t=1.363, n=25, p=0.187
		Rank	t=-3.939, n=5, p=0.158	t=-2.963, n=14, p=0.014*	t=-1.071, n=25, p=0.328
	Other proceptive behaviors	*Color*	t=12.39, n=5, p=0.050*	t=-0.778, n=14, p=0.455	t=2.061, n=25, p=0.050*
		Luminance	t=-12.51, n=5, p=0.050*	t=1.252, n=14, p=0.239	t=2.265, n=25, p=0.050*
		Rank	t=-10.22, n=5, p=0.062	t=-0.047, n=14, p=0.963	t=-0.522, n=25, p=0.607
Female receptive behaviors	*Positive*	*Color*	t=-6.329, n=5, p=0.100	t=1.264, n=14, p=0.236	t=0.771, n=25, p=0.451
		Luminance	t=6.856, n=5, p=0.092	t=-1.821, n=14, p=0.100	t=-1.318, n=25, p=0.204
		Rank	t=0.815, n=5, p=0.565	t=0.203, n=14, p=0.851	t=1.813, n=25, p=0.089
	Consortship interrupted	*Color*	t=-2.437, n=5, p=0.247	t=-0.354, n=14, p=0.731	t=-1.323, n=25, p=0.200
		Luminance	t=2.659, n=5, p=0.228	t=0.080, n=14, p=0.938	t=1.074, n=25, p=0.295
		Rank	t=1.690, n=5, p=0.339	t=0.252, n=14, p=0.806	t=0.386, n=25, p=0.703
	Mount interrupted	*Color*	t=-0.529, n=5, p=0.690	t=1.445, n=14, p=0.186	t=0.506, n=25, p=0.618
		Luminance	t=0.897, n=5, p=0.534	t=-1.965, n=14, p=0.081	t=-0.950, n=25, p=0.353
		Rank	t=0.150, n=5, p=0.905	t=0.077, n=14, p=0.944	t=-0.009, n=25, p=0.993
	Other Negative	*Color*	t=-2.500, n=5, p=0.242	t=0.628, n=14, p=0.545	t=-0.574, n=25, p=0.573
		Luminance	t=3.024, n=5, p=0.203	t=-1.097, n=14, p=0.301	t=0.262, n=25, p=0.796
		Rank	t=-0.109, n=5, p=0.931	t=0.823, n=14, p=0.473	t=-0.830, n=25, p=0.431
Consortship		*Color*	t=260.4, n=5, p=0.001**	t=2.0015, n=14, p=0.078	t=-0.801, n=25, p=0.432
		Luminance	t=-286.9, n=5, p=0.003**	t=-1.629, n=14, p=0.137	t=0.983, n=25, p=0.337
		Rank	t=-387.6, n=5, p=0.002**	t=0.205, n=14, p=0.854	t=-2.963, n=25, p=0.019*
Grooming	Groom	*Color*	t=1.166, n=5, p=0.451	t=2.627, n=14, p=0.025*	t=0.721, n=25, p=0.479
		Luminance	t=-1.121, n=5, p=0.464	t=-2.238, n=14, p=0.049*	t=0.952, n=25, p=0.352
		Rank	t=-1.732, n=5, p=0.333	t=0.720, n=14, p=0.488	t=1.039, n=25, p=0.311
	Groom after copulation	*Color*	t=0.105, n=5, p=0.934	t=2.822, n=14, p=0.017*	t=3.391, n=25, p=0.003**
		Luminance	t=-0.014, n=5, p=0.991	t=2.907, n=14, p=0.014*	t=3.478, n=25, p=0.002**
		Rank	t=-0.134, n=5, p=0.915	t=1.842, n=14, p=0.095	t=1.068, n=25, p=0.397

*: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$.

Table 6.5 Results of GLMM's analyses to assess the relationships between male fecal iT, dominance rank, mating period, and period of social instability (change in alpha male). In all models, male ID was added as a random factor.

	Fecal iT		
	Before rank change Ting-Khao	*After rank change Ting-Khao*	*Entire study period*
Dominance rank	$t=-5.026$, $n=13$, $p<0.001$***	$t=-0.734$, $n=21$, $p=0.475$	$t=-4.128$, $n=34$, $p<0.001$***
No. of receptive females	$t=-0.024$, $n=13$, $p=0.983$	$t=1.243$, $n=21$, $p=0.284$	$t=0.601$, $n=34$, $p=0.567$
Social instability	$t=0.230$, $n=13$, $p=0.830$	$t=-0.013$, $n=21$, $p=0.990$	$t=0.5036$, $n=34$, $p=0.623$

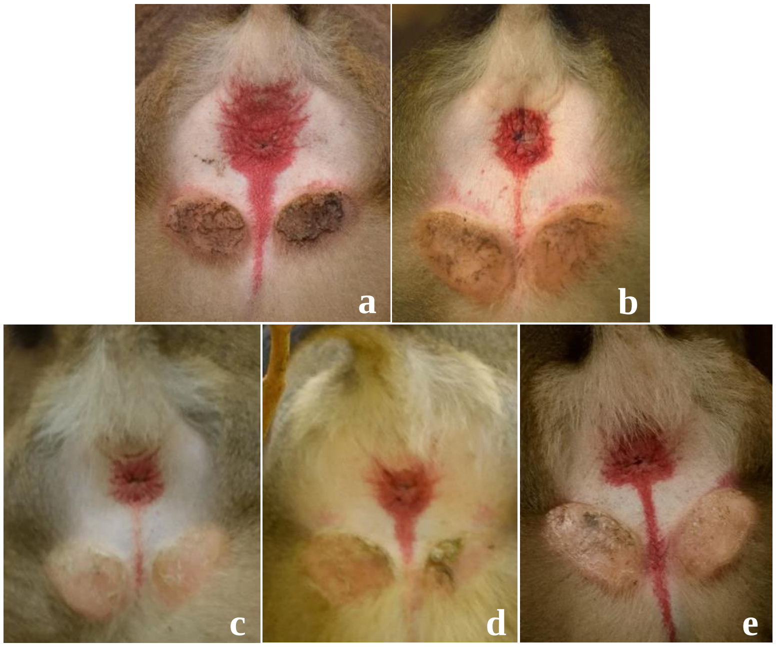


Figure 6.1 Color and pattern variability of male red skin ornaments: (1a) alpha male; (1b) beta male; (1c) third-ranking male; (1d, 1e) two extra-group males. Credit images: Florian Trébouet.

Figure 6.2 (2a) Region of interest (ROI, dashed line) selected in the male anogenital area for color and luminance measurement; (2b) Neutral gray patches (red cross) of the X-rite ColorChecker passport color standard used to standardize RGB measurements from ROI images. Credit images: Florian Trébouet.

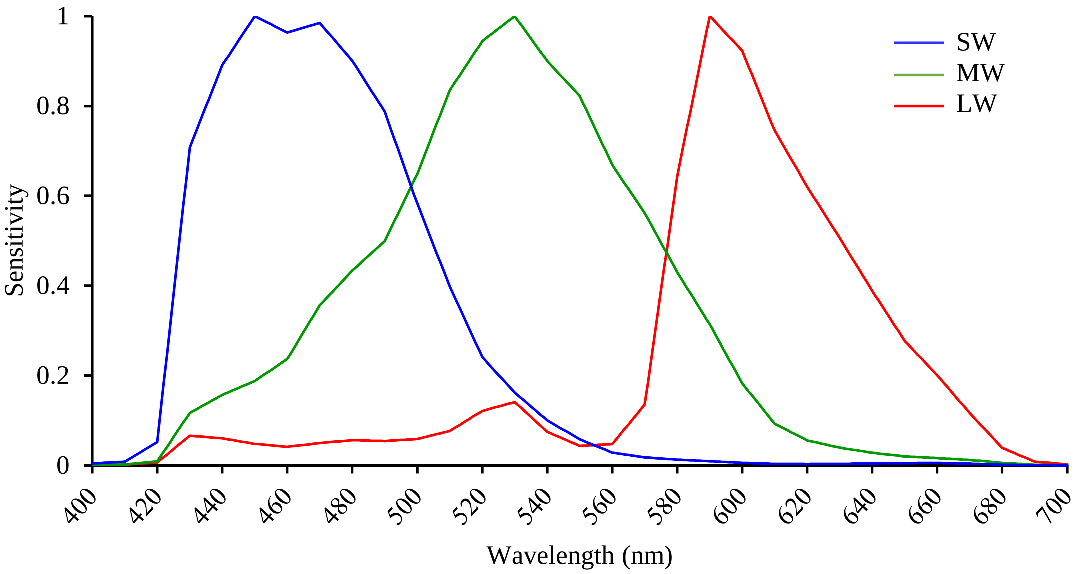


Figure 6.3 Spectral sensitivity of the short (SW), medium (MW), and long (LW) wave receptors for a Nikon D5200 (data from Jiang et al., 2013).

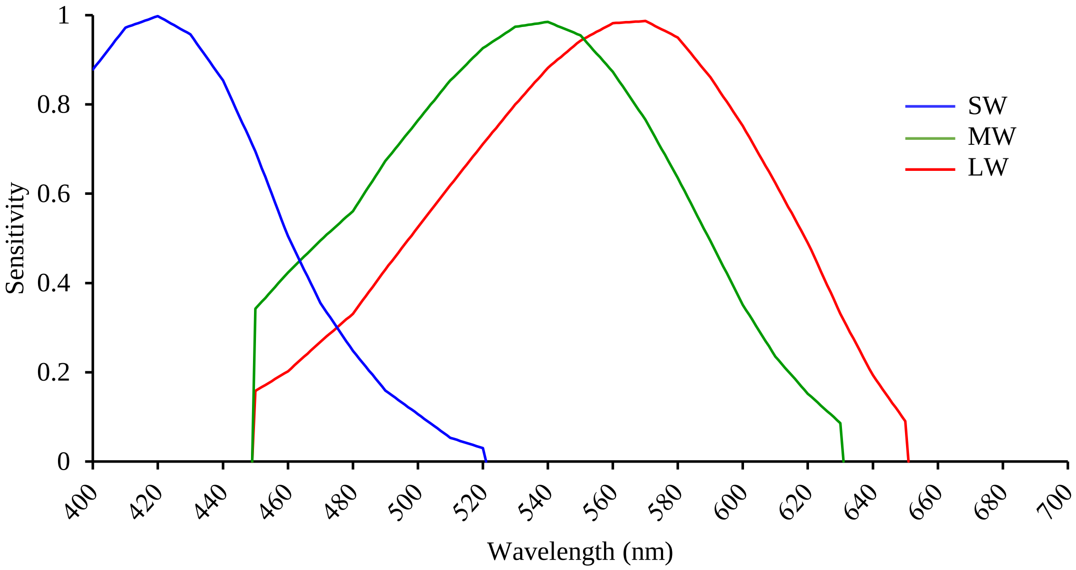


Figure 6.4 Spectral sensitivity of the shortwave (SW) receptor for human (data from Dartnall et al., 1983) and medium (MW), and long (LW) wave receptors for rhesus macaque (*M. mulatta*) (data from Bowmaker et al., 1978). Data were not available over 520 nm for SW receptor and only available between 450-630 nm for MW receptor and 450-650 nm for LW receptor.

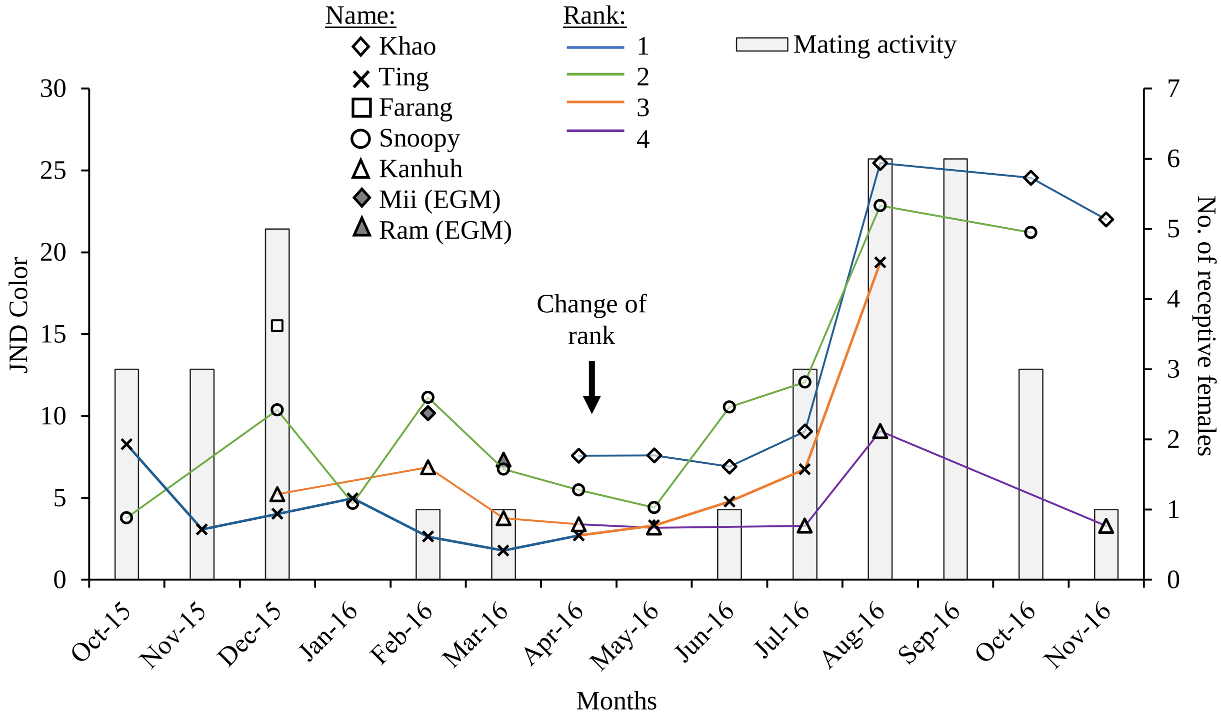


Figure 6.5 Monthly mean maximum JND color variation of the male anogenital color in relation to dominance rank and the number of receptive females.

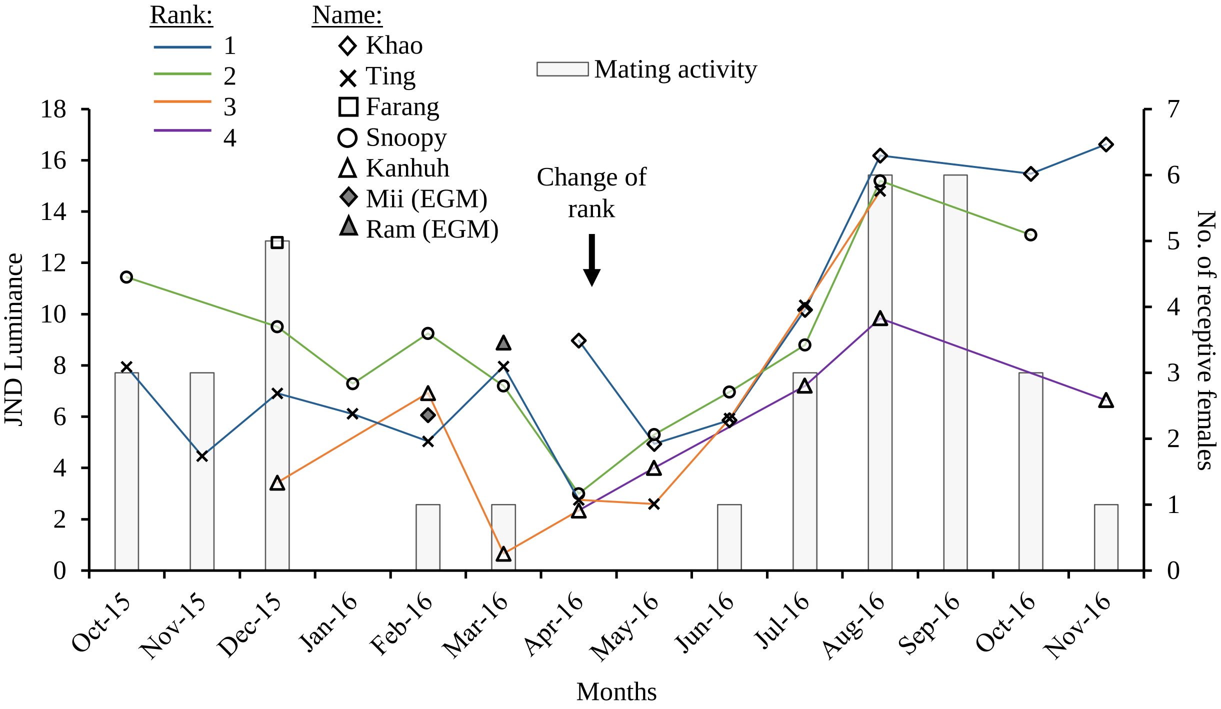


Figure 6.6 Monthly mean maximum JND luminance variation of the male anogenital luminance in relation to dominance rank and the number of receptive females.

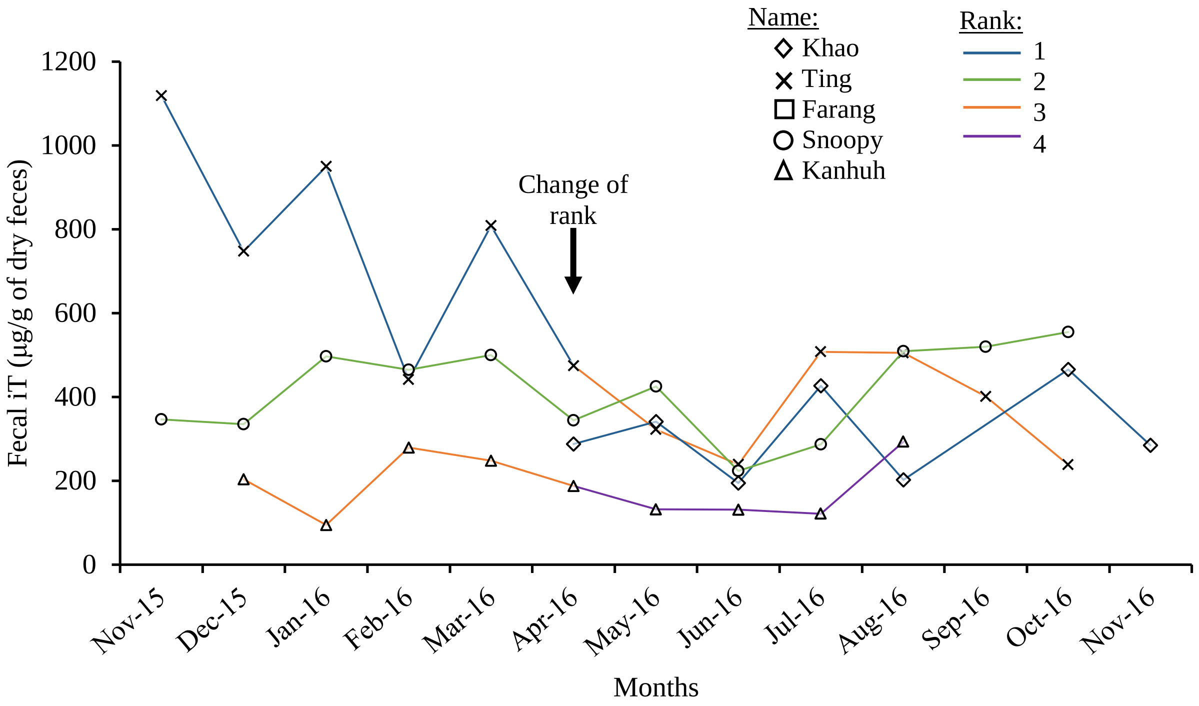


Figure 6.7 Male dominance rank in relation to monthly mean fecal testosterone levels (fecal iT).

CHAPTER 7

GENERAL DISCUSSION

Among multi-male, multi-female primate groups, males usually engage in direct contest competition for access to mates (Clutton-Brock, 2004). Based on their fighting abilities, males are ordered into a dominance hierarchy and the top-ranking male is expected to monopolize access to receptive females depending on the number of simultaneously receptive females in the group (female reproductive synchrony), conceptualized in the Priority-of-Access model (PoA model) (Altmann, 1962). Studies which have tested predictions of the PoA model have found support for the model and concluded that male dominance rank and female reproductive synchrony are good predictors of male reproductive success (Alberts et al., 2006; Boesch et al., 2006; Dubuc et al., 2011; Engelhardt et al., 2006; Setchell et al., 2005a; Sukmak et al., 2014). However, the PoA model is not flawless because a number of proximate factors that impact male's ability to sire offspring in addition to dominance status and female reproductive synchrony are not considered (Alberts, 2012; Alberts et al., 2003; Bissonnette et al., 2011; Port & Kappeler, 2010; Young, Hähndel, et al., 2013).

In this dissertation, I focused on a suite of proximate factors that potentially affect the distribution of mating and reproductive success among males in the poorly studied wild northern pig-tailed macaques (*Macaca leonina*). In this general discussion, I will briefly summarize my main results before developing a general picture of the reproductive tactics of males. I will then expand on the broader implications by comparing my findings to macaque reproductive strategies. Finally, I will provide future perspectives to study reproductive strategies in primates.

7.A. Summary of Results

Knowledge of wild northern pig-tailed macaque populations remains limited, and until now it was still unclear whether the species falls in the category of seasonal or non-seasonal breeders, which is known to be an important factor affecting male and female primate reproductive strategies (Thierry, 2011). In contrast to one previous study that categorized northern pig-tailed macaques as strictly non-seasonal breeder, I found that my study group was best described as moderately seasonal breeder (33-67% of copulations fell within a concise three-month window; see Chapter 3). My group was characterized by two mating peaks in July-September and in December.

The moderately seasonal breeding status of CH group indicates that some females are more likely to overlap during their receptive period, which may affect the relationship between male dominance rank and reproductive success. I tested predictions of the PoA model (Altmann, 1962) in regards to the distribution of mating and reproductive success among males (see Chapter 4). This prediction was supported by the data. The higher up a male was in the dominance hierarchy, the more mating success he had. As predicted by the PoA model, the alpha male achieved the greatest share of paternity among males (36.4%) but his ability to monopolize receptive females was limited by female reproductive synchrony. In contrast to model predictions, high-ranking males were less successful and lower-ranking males were more successful in obtaining matings. In terms of reproductive success, the alpha male, and especially the beta male, did not gain as much paternity as predicted by the PoA model. Furthermore, an unexpected high number of extra-group males (EGMs), excluded from the PoA model, controlled a relatively large proportion of paternity (45.5%), despite a low observed mating success (4.1%). Overall, the PoA model adequately predicted male reproductive success, reinforcing that female reproductive synchrony plays a major role in reducing an alpha male's ability to monopolize receptive females. However, other proximate factors not included in the PoA model can additionally limit the monopoly by high-ranking males.

Among proximate factors proposed to explain the residual variation from the mating/reproductive success predicted by the PoA model, I identified energetic constraint of male mate-guarding, sexual activity of lower-ranking males as well as EGMs, and the intensity of female mate choice (see Chapter 5). Against a background of these factors, I identified different male mating tactics in northern pig-tailed macaques (described in detail in the following section). Briefly, high-ranking males attempt to monopolize access to receptive females through forming long-lasting consortships and directly fending off lower-ranking males. When a female is not mate-guarded by a high-ranking male, other males can engage with females through alternative mating tactics, like surreptitious copulations and short-term consortships out of sight of high-ranking resident males. However, I also observed that one EGM (Chuan) was able to directly approach and copulate with a receptive female in full sight of resident males. I considered this male super-dominant because they could not be defeated or interrupted by even the highest-ranking male in the group. I also found evidence that female mate choice affects male reproductive tactics (described in detail in the following section). On nine occasions, I observed receptive females who, after temporarily leaving the group, actively approached and copulated with five EGMs (Aran, Boo, Chuan, Drogo, and Manu). Two receptive females also went absent from the group during most of their receptive periods and copulated with EGMs (Chuan and Manu).

In addition, I investigated the adaptive function of male red ornaments in northern pig-tailed macaques (see Chapter 6). Data analyses supported that male red skin coloration functions as an ornament attractive to females. Darker and redder males had more mating partners and received more proceptive behaviors than lighter and less red males. In addition, red ornaments may also act as a badge of status, although evidence supporting this hypothesis was mixed, because no effect of testosterone levels on male red ornaments nor a relationship between testosterone and dominance rank, social instability, or mating activity was found.

7.B. Summary of Male Reproductive Tactics in Northern Pig-tailed Macaques

In macaques, male dispersal and mating competition lead to a variance in reproductive success greater in males than in females (Clutton-Brock, 1988; Thierry, 2011). While females are usually philopatric and reproduce in their natal group, males emigrate and reproduce in neighboring groups (Bercovitch & Harvey, 2004). Long-term studies have shown that the lifetime reproductive success of females mostly depends on their longevity (e.g., Japanese macaques, *M. fuscata*, Fedigan, Fedigan, Gouzoules, Gouzoules, & Koyama, 1986; rhesus macaques, *M. mulatta*, Bercovitch & Berard, 1993), but other factors affect the lifetime reproductive success of males (Thierry, 2011). Young males often disperse from their natal group before or soon after reaching sexual maturity, and often immigrate directly into a neighboring group with same aged-peers (van Noordwijk & van Schaik, 1985; Zhao, 1996). In some species, young males may alternatively join small all-male bands (e.g., rhesus macaques, Drickamer & Vessey, 1973; Japanese macaques, Sugiyama, 1976; Formosan macaques, *M. cyclopis*, Hsu & Lin, 2001) or become semi-solitary for few months (e.g., long-tailed macaques, *M. fascicularis,* van Noordwijk & van Schaik, 1985; Tibetan macaques, *M. thibetana*, Zhao, 1996) or even few years (e.g., rhesus macaques, Drickamer & Vessey, 1973; Japanese macaques, Sugiyama, 1976). In my study, I observed the presence of semi-solitary EGMs, but I did not find any evidence to support the existence of all-male bands (see Chapter 3). However, the absence of observation of all-male bands could be an artifact of observation bias because my study only focused on one bisexual group and occasional encounters of what seemed to be semi-solitary males. Dispersal of males is not limited to young males but is seen also in adult, older males who may continue to migrate multiple times over their reproductive life span (e.g., Japanese macaques, Sugiyama, 1976; Tibetan macaques, Zhao, 1996; rhesus macaques, Berard, 1999).

In northern pig-tailed macaques, I considered that, once a young male emigrates from a group, he is facing two choices, either immigrate into another group (i.e., a multi-male, multi-female group) or live as a semi-solitary male (Thierry, 2011). Furthermore, based on the PoA model (Altmann, 1962), I considered that: 1) all males should compete for a high dominance position and particularly the top-ranking, alpha male position within the male dominance hierarchy, which should offer one of the highest male reproductive success; and 2) males who do not hold the alpha position should find a way to access receptive females through alternative mating tactics: either as a subordinate resident male or as a semi-solitary EGM by visiting frequently different groups.

Based on these assumptions and my results, I divided male reproductive tactics of northern pig-tailed macaques into four main tactics, which are represented in Figure 7.1 and described below:

1) Top-ranking resident male tactic: The male migrates into a new group, and thereafter directly challenge the highest-ranking male through direct contest competition (based on fighting abilities). The dominant male of a group has priority of access to mate with receptive females and mate-guard them through long consortships and multiple-mount copulations. However, when more than one female is simultaneously receptive, even the strongest alpha male will unlikely be able to monopolize all females' copulations. The alpha male will have to share copulations with the next-highest ranking males. The ability of the dominant male to control access to females may also depend on the experience and history of the individual and female mate choice. In long-tailed macaques, this male tactic is called the "bluff immigrant" tactic and is considered risky because males may be injured or die during an attempt to take over the alpha male position (van Noordwijk & van Schaik, 1985). Only full-grown males at their prime age should be expected to be the most successful bluff immigrant because of their supposedly higher fighting abilities (e.g., Japanese macaques, Sprague, 1992; Sprague et al., 1998; long-tailed macaques, van Noordwijk & van Schaik, 1985). Despite these risks, the top-ranking resident male tactic offers one of the highest male reproductive success values.

2) Lower-ranking resident male tactic: The male migrates into a new group, enters the male dominance hierarchy at the bottom and does not challenge the alpha male. When more than one female is simultaneously receptive, lower-ranking males (adults and subadults) are able to mate with receptive females when the receptive female is not in a continuous and close consortship with a high-ranking male. Subordinate males (adults but mostly subadults) engage in short,

opportunistic, surreptitious consortships and copulations, out of sight of higher-ranking males. To avoid direct competition, they may follow a receptive female during a consortship with a higher-ranking male and wait for the female to be out of sight of the higher-ranking male to copulate with her. Depending on the number of simultaneously receptive females and the male's dominance rank, males higher up in the dominance hierarchy (e.g., beta male or third-ranking male) may engage in long consortship and copulations with a receptive female when the top-ranking male is already consorting another receptive female. In long-tailed macaques, this male tactic has been termed "unobtrusive immigrant" tactic and is considered less risky than the dominant resident male tactic (bluff immigrant tactic) because direct contest competition with a high-ranking male is avoided (van Noordwijk & van Schaik, 1985). This tactic is expected to be followed by males of all ages. The reproductive success of males following this tactic is likely to be lower and to show greater variation than the top-resident male tactic. Furthermore, for males following this tactic, reproductive success also depends on the male's experience and female mate choice (for further details, see Chapter 5).

3) Subordinate EGM tactic: After emigrating, a male may live a semi-solitary life, perhaps for months or even years. Subordinate EGMs (e.g., Aran, Boo, Drogo, and Manu; see Chapter 5) may monitor groups to detect mating periods (i.e., when more than one female is simultaneously receptive) by roaming and visiting the groups' periphery, and wait for receptive females to approach them. Similar to the lower-ranking resident male tactic, subordinate EGMs would engage in short, surreptitious copulations with receptive females at the periphery of the group, out of resident adult males' sight. However, depending on female mate choice, EGMs may also engage in long copulations and consortships with receptive females if these females approach them and travel away from the group for hours, days, or possibly during a female's entire

receptive period. A subordinate EGM tactic may lead to a less predictable and probably low level of reproductive success because of their more limited access to receptive females than resident males. This tactic also depends on the male's experience, female mate choice, and the degree of female reproductive synchrony of a group (for further details, see Chapter 5). However, in contrast to the resident male tactic, it is likely that a life of a semi-solitary EGM is more costly because of increased predation risks and starvation due to greater difficulty to access food resources (e.g., savanna baboons, *Papio cynocephalus*, Alberts & Altmann, 1995).

4) Super-dominant EGM tactic: The tactic is similar to the subordinate EGM tactic but differs in one important aspect. So-called "super-dominant" EGMs (e.g., Chuan; see Chapter 5) do not wait for receptive females to approach them at the periphery of a group but instead may directly enter a group and establish proximity with a receptive female in full sight of resident males. Despite facing agonistic behaviors from resident males, super-dominant EGMs successfully fight back and maintain proximity with receptive females. Therefore, the mating pattern of super-dominant EGMs should be similar to that of high-ranking resident males characterized by long consortships and copulations. The super-dominant EGM tactic should lead to high reproductive success because of the supposedly unlimited access to receptive females of not only one, but as many groups as EGMs can monitor. However, the risk associated with this tactic is potentially high because of the semi-solitary life (see previous tactic). This tactic also depends on the male's experience, female mate choice, and the degree of female reproductive synchrony of a group.

In this study, EGMs were mainly observed at the periphery of the group during the mating peak when the number of simultaneously receptive females is greater than one. Because of the moderately seasonally breeding status of my study group, EGMs are more likely to follow a tactic that Henzi and Lawes (1988) identified as "hovering" EGM tactic. Hovering EGMs monitor specific groups to increase interaction probability with females and ensure copulations when they are receptive during a mating peak. Thus, EGMs are expected to monitor those groups and wait for the mating peak when the alpha male of the group cannot monopolize all receptive females. In my study, three EGMs (Aran, Ram, and Mii) were observed repeatedly at the periphery of the group even when no female was receptive, suggesting that the same EGMs visited several times the group to monitor the females' reproductive status (see Chapter 5). Furthermore, EGMs were more often observed at the periphery of the group during the mating peak. The EGM tactics could be either a lifetime tactic or a temporary tactic, ending when they migrate into a new group by challenging the top-ranking male or by entering as a low-ranking male. These results highlighted the importance of considering EGMs as part of the male mating tactics and that the social group is not equivalent to the reproductive unit in primates.

In addition, I found evidence that female mate choice affects male reproductive tactics in northern pig-tailed macaques: 1) receptive females mate promiscuously, especially when female reproductive synchrony is relatively high in the group; 2) receptive females maintain long consortships (hours to days) and copulate with high-ranking males; 3) receptive females actively engage in surreptitious copulations with lower-ranking males; 4) receptive females approach and copulate with EGMs out of sight of resident males and may maintain long consortships with them (hours to days); and 5) receptive females seem to be attracted to darker and redder males.

Altogether, these finding highlighted the complex interactions of both male and female reproductive strategies. While males compete for access to mates through direct contest competition and alternative reproductive tactics in northern pig-tailed macaques, the degree of female reproductive synchrony and female mate choice additionally explain a great variance of male reproductive success.

7.C. Contributions to Macaque Reproductive Strategies

Macaques are an interesting group for studying interrelationships of individual mating strategies, because they are characterized by varying degrees of dominance asymmetry, various male reproductive skew, and a wide variability of mating strategies (Soltis, 2004; Thierry, 2011). The more or less periodic nature of macaque's reproduction is one main factor that has been identified to explain the broad diversity of male mating system in macaques (Thierry, 2007). Indeed, because of their wide geographical distribution ranging from temperate to tropical regions, macaques present seasonal variation of reproduction (Fooden, 1980).

In macaque species living in the tropics, reproduction typically occurs year-round and such species are typically classified as non-seasonal breeders. The number of simultaneously receptive females is low with only one receptive female at any given time in the group (e.g., Tonkean macaques, *M. tonkeana*, Paul, 2004; Thierry, Anderson, Demaria, Desportes, & Petit, 1994). Thus, the top-ranking male copulates with the receptive females during long-lasting consortship (days or weeks) and controls most of the paternity (Thierry, 2011). In such context, the development of alternative male mating tactics and female direct mate choice are limited. In Tonkean macaques, one of the Sulawesi macaque species (Aujard, Heistermann, Thierry, & Hodges, 1998; Thierry et al., 1994), the alpha and beta males maintained exclusive and enduring associations with receptive females, excluding lower-ranking males from mating. Due to the high reproductive skew, male mating competition is through direct contest competition based on fighting abilities (Soltis, 2004). Indeed, higher-ranking males often aggressively interrupt the mating attempts by lower-ranking males (Soltis, 2004).

In macaque species living in temperate regions, a strong effect of environmental seasonality influences female reproductive patterns with female reproductive synchrony being more common. The availability of food resources fluctuates between seasons leading to corresponding fluctuation in female reproduction and to females becoming synchronized in their nutritional needs accordingly (Thierry, 2007; Zhao, 1996). Typically, females are receptive during a discrete period of two-to-three months centered in the fall (Soltis, 2004; Thierry, 2011). More than one female is likely to be synchronously receptive, limiting mate-guarding by the top-ranking male (Bissonnette et al., 2011). Consortships between males and receptive females may occur but often last only few hours, and short copulations are more likely. To access receptive females, males do not solely engage in agonistic competition but may compete through endurance rivalry or tenure (e.g., rhesus macaques, Bercovitch, 1997; Higham, Heistermann, & Maestripieri, 2011; see also Thierry, 2011). Because of the limited ability of a high-ranking male to monopolize receptive females, there is more room for the development of alternative male reproductive tactics and the expression of female mate choice. For instance, in Barbary macaques (*M. sylvanus*), mating and reproductive skew towards the high-ranking males are modest and lower-ranking, post-prime males formed leveling coalitions to exclude high-ranking, prime males from receptive females, which increased their mating access (Bissonnette et al., 2011). Females also show preference to copulate with middle- or low-ranking males (e.g., rhesus macaques, Chapais, 1983; Japanese macaques, Soltis et al., 2001) or with males exhibiting darker and redder faces (e.g., rhesus macaques, Dubuc, Allen, et al., 2014). In strictly seasonal breeding species, the distribution of paternity is thus more variable and lower-ranking males may have higher reproductive success than high-ranking males (e.g., 0-12.5% of paternity controlled by the alpha male, rhesus macaques, Dubuc et al., 2011; 33%, Japanese macaques, Soltis et al., 2001; 0-25%, Barbary macaques, Kuester & Paul, 1996; Kümmerli & Martin, 2005; Modolo & Martin, 2008; reviewed by Bissonnette et al., 2011).

However, despite this dichotomic classification of macaques' periodicity of reproduction (seasonal breeder vs. non-seasonal breeder) being helpful to explain reproductive strategies in some species, it also misrepresents others with more complex mating systems. Indeed, a number of macaque species living in tropical or semitropical regions are often considered as non-seasonal breeders when at least some populations are moderately seasonal breeders (i.e., 33-67% of births occur within a three-month period, van Schaik et al., 1999). For instance, lion-tailed macaques (*M. silenus*) is considered non-seasonal breeder with year-round births but 60% of births recorded by Singh and colleagues (2006) occurred between January-March in eight wild groups. In northern pig-tailed macaques, I found that 41% of births occurred between April-June (see Chapter 3) and in three wild groups of long-tailed macaques, 49% of births occurred between August-October (van Noordwijk & van Schaik, 1999); all indicating moderate seasonality despite the fact that these species have previously been considered non-seasonal breeders (reviewed by Bercovitch & Harvey, 2004; Thierry, 2011). In the Sulawesi species group, crested macaques (*M. nigra*, Marty, 2015) and Moor macaques (*M. maurus*, Okamoto, Matsumura, & Watanabe, 2000; Tokuda et al., 1968) are also both moderately seasonal breeders with 33-67% and 56% of all births occurring in a three-month period, respectively. Apart from Tonkean macaques who is strictly non-seasonal breeder (Paul, 2004), data are still missing about the reproductive seasonality of the other species of Sulawesi (i.e., Gorontalo macaques, *M. nigrescens*, Heck's macaques, *M. hecki*, and booted macaques, *M. ochreata*).

The degree of reproductive seasonality of a species may still be variable between different populations and even between seasons. For instance, while births were evenly distributed throughout the year in five wild populations of northern pig-tailed macaques in Bangladesh, birth peaks were reported in wild populations in northeastern India and in the present study (see Chapter 3). In long-tailed macaques, the degree of seasonality varied greatly between 37-78% of births occurring within a 3-month period in different groups (van Noordwijk, 1985a; van Noordwijk & van Schaik, 1999; van Schaik & van Noordwijk, 1985). In moderately seasonally breeding species, female reproductive synchrony is thus less predictable than in strictly non-seasonal breeding species (e.g., Tonkean macaques, Paul, 2004; Thierry et al., 1994) and may be more season dependent as in strictly seasonal breeding species (Thierry, 2007; Zhao, 1996). Consequently, in moderately seasonally breeding species, what mating pattern should we expect to find? A mating pattern closer to strictly seasonal breeding species or strictly non-seasonal breeding species or a combination of both?

The crucial variable is thus not reproductive seasonality per se but the degree of female reproductive synchrony, which will determine the mating pattern in a group. As female reproductive synchrony may vary from one or several simultaneously receptive females in moderately seasonally breeding species, the extent to which the alpha male can monopolize receptive females through consortship is consequently variable. Despite reports of mating peaks in one group of long-tailed macaques, the female reproductive synchrony was relatively low and the alpha male was thus able to control almost all matings and copulations (alpha male's paternity: 67% of offspring, Engelhardt et al., 2006). Despite living in large group size (>100 individuals, Marty, 2015), high-ranking males in crested macaques were able to monopolize copulations with receptive females due to the low female reproductive synchrony, leading to a high reproductive skew towards the alpha male (on average 65% of paternity, Engelhardt et al., 2017). In both species, the high alpha male's reproductive success was thus attributed to a low female reproductive synchrony (Engelhardt et al., 2006; Engelhardt et al., 2017), but also to the male ability to detect females' fertile phases (Engelhardt et al., 2004; Higham et al., 2012). Indeed, by assessing a female's fertile phase, the alpha male mate-guarded the female more intensively during her fertile phase, increasing greatly his likelihood to father her offspring (Engelhardt et al., 2004; Higham et al., 2012).

Furthermore, in crested macaques, male mating competition is extremely high, leading to one of the most extreme canine dimorphisms in primates (male-female ratio of canine size: 2.61, Plavcan & van Schaik, 1992). Males compete for dominance through escalated fights and severe injuries (Marty, Hodges, Agil, & Engelhardt, 2017) and tenure of the alpha male is an average of 12 months (Marty et al., 2017), one of the shortest of any primate species (average of 50 months in multi-male, multi-female primate groups, Lukas & Clutton-Brock, 2014). Similarly, in another Sulawesi macaques, Moor macaques, mating skew is reported to be high towards the alpha male in a captive study (79% of copulations, Matsumura, 1993), but the absence of genetic paternity data could not confirm whether this high mating skew translated into high reproductive skew for the alpha male. Because of the low female reproductive synchrony, the mating patterns of long-tailed macaques, crested macaques, and Moor macaques, all species considered to show moderate breeding seasonality, resemble, as expected, to the mating pattern found in the strictly non-seasonal breeding species Tonkean macaques (Thierry et al., 1994).

However, not all moderately seasonally breeding species can be characterized by the same mating pattern, and variation across populations of a same species can also be found. For instance, in northern pig-tailed macaques (see Chapter 4), I found that the alpha male, despite being the most successful, controlled only 36.4% of the paternity in the group. This reproductive skew was closer to what has been found in some strictly seasonal breeding species (e.g., 0-38%, Barbary macaques, reviewed by Bissonnette et al., 2011; 43%, toque macaques, Keane et al., 1997; 33%, Japanese macaques, Soltis et al., 2001). Indeed, despite that the high-ranking males in my study group (see Chapter 5) engaged in longer copulations and consortships and enjoyed the highest mating success, other males were able to successfully access receptive females when the number of simultaneously receptive females exceeded one. Such results were also found in the closely related species southern pig-tailed macaques (Oi, 1996) but also in long-tailed macaques (van Schaik & van Noordwijk, 1985). The effect of male dominance rank on the variation in mating and reproductive success may be diluted by alternative male mating tactics and female mate choice. For instance, when receptive female were simultaneously receptive, surreptitious copulations between receptive females and lower-ranking males were observed in northern pig-tailed macaques (see Chapter 4) and southern pig-tailed macaques (Caldecott, 1986; Oi, 1996), as well as between receptive females and EGMs in northern pig-tailed macaques (see Chapter 4) and long-tailed macaques (van Noordwijk, 1985a). Such matting tactics are usually found in strictly seasonally breeding species such as rhesus macaques (e.g., Chapais, 1983, Berard et al 1994) and Japanese macaques (Soltis et al., 2001). Furthermore, in northern pig-tailed macaques (see Chapter 6), I found evidence that receptive females prefer to copulate with males exhibiting darker and redder anogenital coloration. Such evidence of female attraction to male red ornament was also found in rhesus macaques, in which female mate choice led to the development of male facial color with darker red males being more attractive to females in a mating context (Dubuc, Allen, et al., 2014). Thus, as female reproductive synchrony increases in moderately seasonally breeding species, mating patterns become more similar to patterns found in strictly seasonal breeding species.

Because of the great variation of female reproductive synchrony seen in moderately seasonally breeding species, mating and reproductive skew are also expected to vary between populations of a same species and between seasons. In crested macaques, the proportion of alpha male paternity varied considerably among three groups over three consecutive years, ranging between 29-100% (Engelhardt et al., 2017). This variation of paternity was attributed to a variation of female reproductive synchrony across groups, directly affecting the alpha male’s ability to monopolize receptive females. In northern pig-tailed macaques, the difference of mating distribution among males between CH group (see Chapter 4) and HQ group (Carlson, 2011) was also likely attributable to a difference of the extent of female reproductive synchrony. Additionally, differences in alpha males’ personality/experience and female mating preference for the alpha male may further explain the difference of alpha males’ mating success between those two groups and within CH group with an alpha male change. Thus, even within a species, the matting pattern and alpha male’s reproductive skew may vary between populations because of variation in female reproductive synchrony, which in turn may depend on environmental conditions such as rainfall (Caldecott, 1986).

The defendability of receptive females, and thus the expression of male mating tactics, has also been related to the operational sex ratio (OSR) of a group/population, which is the ratio of fertilizable females to sexually active resident males (Emlen & Oring, 1977). When the number of simultaneously receptive females is relatively small compared to the number of sexually active resident males (low OSR), resident males according to dominance rank are expected to successfully defend receptive females from extra-group males, and thus monopolize mating access to receptive females (Takahashi, 2001). Inversely, when the OSR is high, resident males following alternative mating tactics and extra-group males are predicted to be able to copulate with receptive females because of the inability of the top-ranking resident male to control access to all receptive females. Such predictions were directly tested and supported in the seasonally breeding species Japanese macaques (Takahashi, 2001). In the study, EGMs were more likely to copulate with receptive females when there were two-to-three times more receptive females per resident adult male (Takahashi, 2001). However, I found contrasting results in this dissertation. My findings (see Chapter 4 and 5) indicated that, when EGMs were observed copulating with receptive females, there were on average 2.4 receptive females per day for six-to-nine sexually active males in the group during the mating periods, which was then equivalent to a relatively low OSR. Thus, in northern pig-tailed macaques, access to receptive females by EGMs was still possible in a group with a low OSR. Two explanations for such a result might be that: 1) the mating success of EGMs may be more dependent on female mate choice than male-male competition, that is an extension of OSR; and 2) super-dominant EGMs may be dominant over resident adult males, allowing those EGMs to freely access receptive females (see above super-dominant EGM tactic, see also Chapter 5). Likewise, in toque macaques, EGMs were not more successful at fathering offspring in one-male groups than in multimale groups, and the success of EGMs was more likely related to female mate choice (Keane et al., 1997). Female mate choice for EGMs has also been reported in the strictly seasonal breeders Japanese macaques (Inoue & Takenaka, 2008; Sprague, 1991b) and rhesus macaques (Berard et al., 1994; Brereton, 1981), and in the moderately seasonal breeder long-tailed macaques (van Noordwijk, 1985a). Thus, EGMs seem more likely to be able to access receptive females in strictly or moderately seasonally breeding populations, in which females have more freedom to choose mates.

Because female macaques often mate polyandrously in strictly and moderately seasonally breeding species, paternity could also be determined at the postcopulatory level though sperm competition and cryptic female choice (Brauch et al., 2008; Engelhardt et al., 2006; Soltis, 2004). Consistent with sperm competition theory, primates living in multi-male, multi-female groups, (such as macaques) have high testis-to-body weight ratios (Dixson, 2012; Harcourt et al., 1981; Soltis, 2004) and a high number of viable sperm in male ejaculates (Schrod, 2002). Further, the differences in sperm number, vitality and/or viability has been recognized to potentially affect conception in primates (Eberhardt, 1996; Reeder, 2003). For instance, in rhesus macaques, male testes increases in volume by 50-70% during the mating season (Sade, 1964; Wickings & Nieschlag, 1980) and males who had larger testes relative to body weight sired more offspring (Bercovitch & Nürnberg, 1996, 1997). In long-tailed macaques, females seem to prefer mating with several males in relatively fast succession (Nikitopoulos, Heistermann, de Vries, van Hooff, & Sterck, 2005), which may increase sperm competition and benefit the females (Engelhardt et al., 2006). The potential benefits that females might indirectly receive are various (reviewed by Engelhardt et al., 2006): avoiding inbreeding or genetic incompatibilities (Newcomer, Zeh, & Zeh, 1999; Tregenza & Wedell, 2002; Zeh & Zeh, 2001), receiving good sperm (“good-sperm” model, Yasui, 1997), and facilitating cryptic female choice (Eberhardt, 1996). However, there is still a general paucity of knowledge of the postcopulatory mechanisms in primates and to what extent they play a role for male reproductive success (Setchell, 2016). This paucity is mainly due to the difficulties of conducting such experimental studies (Setchell, 2016).

Thus, moderately seasonally breeding species in macaques represent excellent models to study details of male and female reproductive strategies because of the wide range of female reproductive synchrony patterns, which strongly affect the alpha male’s ability to control access to receptive females. As expected, when female reproductive synchrony is low in moderately seasonally breeding populations, the mating pattern resembles ones found in strictly non-seasonally breeding species, characterized by high reproductive skew towards the alpha male. Inversely, when female reproductive synchrony is high, the mating pattern of moderately seasonally breeding populations resemble ones found in strictly seasonally breeding species, characterized by the expression of: 1) alternative male reproductive tactics to avoid direct competition with high-ranking males; 2) female mate choice; and most likely 3) postcopulatory mechanisms (sperm competition, female cryptic choice). Independent of female reproductive synchrony, the alpha male still gains the highest reproductive success in moderately seasonally breeding macaques. Thus, male competition for dominance is expected to be high, which is consistent with the pronounced sexual dimorphism found in those species (Thierry, 2011). However, more studies on the mating patterns of moderately seasonally breeding macaques are still needed, especially in the Mentawai macaques, the majority of Sulawesi macaques, southern pig-tailed macaques, and lion-tailed macaques, in which mating and paternity data are almost absent. Furthermore, comparative analyses of long-term field studies between different populations of a same species are lacking. For instance, most mating behaviors and paternity data of northern pig-tailed macaques (this study; Carlson, 2011), long-tailed macaques (Engelhardt et al., 2006; van Noordwijk, 1985a), and crested macaques (Engelhardt et al., 2017; Marty, 2015; Marty et al., 2017) come from only one population at one field site. Because of environmental factors that may affect female reproductive synchrony between populations, the mating patterns may vary between populations and over time. Consequently, studies from only one population may be misrepresentative of the species’ mating pattern, highlighting the importance of conducting studies on different population.

7.D. Conclusions

To provide a comprehensive picture of male reproductive tactics in northern pig-tailed macaques, this dissertation highlighted the importance of coupling morphological, hormonal, and genetic paternity analyses with behavioral and demographic data collected in the field. The emerging picture of male mating tactics of northern pig-tailed macaques is a complex one. To gain reproductive success, males engage in a diversity of mating tactics, strongly influenced by male dominance rank and the degree of female reproductive synchrony. Based on a 22-month field study using data collected non-invasively, my results largely support predictions of the PoA model in revealing a positive relationship between male dominance rank and mating success. However, the distribution of male reproductive success indicated that: 1) the alpha male controlled a proportion of paternity much lower than predicted by the PoA model; and 2) EGMs, not considered a relevant variable in the traditional PoA model controlled a relatively large proportion of paternity despite a low mating success. This is the first study to report mating and successful paternity by EGMs in a moderately seasonally breeding species with a year-round bisexual group structure. Such results forced us to include EGMs as an integral part of male mating tactics in primates.

Overall, I was able to identify four male mating tactics: 1) the top-ranking resident male tactic; 2) the lower-ranking resident male tactic; 3) the subordinate EGM tactic; and 4) the super-dominant EGM tactic. In addition, I found evidence of female mate choice for specific males, which indicates the complex interaction between male and female reproductive strategies. In particular, some evidence suggested that red ornamentation exhibited in the male’s anogenital area is attractive to females. Thus, this dissertation is the first study that investigated the adaptive function of the male red ornament in northern pig-tailed macaques.

Altogether, this dissertation provided a comprehensive picture of fundamental components of sexual selection—mate competition and mate choice—and contributed to a better assessment of the ultimate function of male secondary sexual characteristics. This study highlighted the need to develop an extended version of the PoA model by including additional proximate factors such as mate-guarding costs, surreptitious copulations by lower-ranking males and EGMs, and female mate choice. This study also helped to fill a gap in the existing literature of cercopithecine sexual selection and added knowledge to any discussion or comparative analysis concerning hypotheses derived from sexual selection theory—one of the greatest and most enigmatic achievements of Charles Darwin.

7.E. Future Directions

This dissertation not only highlighted the complexity and diversity of male reproductive tactics but also raised new questions and directions for future research to further improve our understanding of sexual selection in northern pig-tailed macaques and other primates. These future directions are listed as follow:

1. The PoA model has only been thoroughly studied in a handful of primate species. Despite being a good model, there are other important proximate factors that may explain deviations from the PoA model. Because such factors are probably dependent of the demography and social system of the population and the species (e.g., Alberts et al., 2003; Setchell, Charpentier, & Wickings, 2005b), tests of the PoA model are needed in a wide variety of primate species in

different locations to assess the proximate factors affecting mating and reproductive success (Bissonnette et al., 2011), which could lead to the formulation of a more comprehensive PoA model.

2. The evidence of female mate choice found in this dissertation indicates that a comprehensive study including behavioral, morphological, and hormonal analyses is much needed to focus on female reproductive strategies in northern pig-tailed macaques. Indeed, females exhibit sex skin swelling and reddening during the periovulatory period but no detailed study has yet tested the role of sexual swellings in female northern pigtailed macaques. Studies need to look at how the development of female sex skin swelling relates to hormonal levels, and whether males rely on female sex skin swelling as an indicator of female quality ("reliable indicator" hypothesis, Pagel, 1994) or fertility ("graded-signal" hypothesis, Nunn, 1999a). The need to determine whether males are able to detect a female's fertile phase is crucial. As dominant males may time their mating effort to the female's fertile phase (e.g., Engelhardt et al., 2006; Heistermann et al., 2008; Higham et al., 2012), considering the entire receptive period instead of just the shorter female's fertile period may have resulted in obscuring more subtle male mating tactics focused on just the females' fertile phase.

3. A larger sample size of male color ornaments and long-term genetic paternity data are needed to further investigate: 1) whether red skin ornament functions as an honest signal of the male's condition, a badge of status, or both at the same time; and 2) whether and to what extent male qualities are linked to this signal. Further studies are also needed to elucidate the relationship between color, shape, and size of the red sex skin in males. Indeed, other characteristics that I did not measure in this study, such as interindividual differences in size and patterns of the male red ornament, are worth being investigated to assess whether it may affect female mate choice.

4. This dissertation highlighted the important contribution of EGMs to the male reproductive success but little is known on the different choices that a male may take to disperse, the costs (access to resources, risk of predation) and benefits (reproductive success) of EGM mating tactics, and how EGMs optimize their reproductive success in northern pig-tailed macaques and other multimale, multifemale primate-living groups. Furthermore, the existence of all-male bands in northern pig-tailed macaques remains to be confirmed.

5. Four male mating tactics were identified in northern pig-tailed macaques, but the temporal aspects of these tactics remain to be studied, especially in EGMs. Long-term studies are thus needed to investigate whether these male tactics are temporary or permanent. For instance, there is no data to support whether EGM tactics last for months, years, or the entire male's life span. Temporal variation of male mating tactics is important to consider because of their great effect on the lifetime reproductive success of an individual.

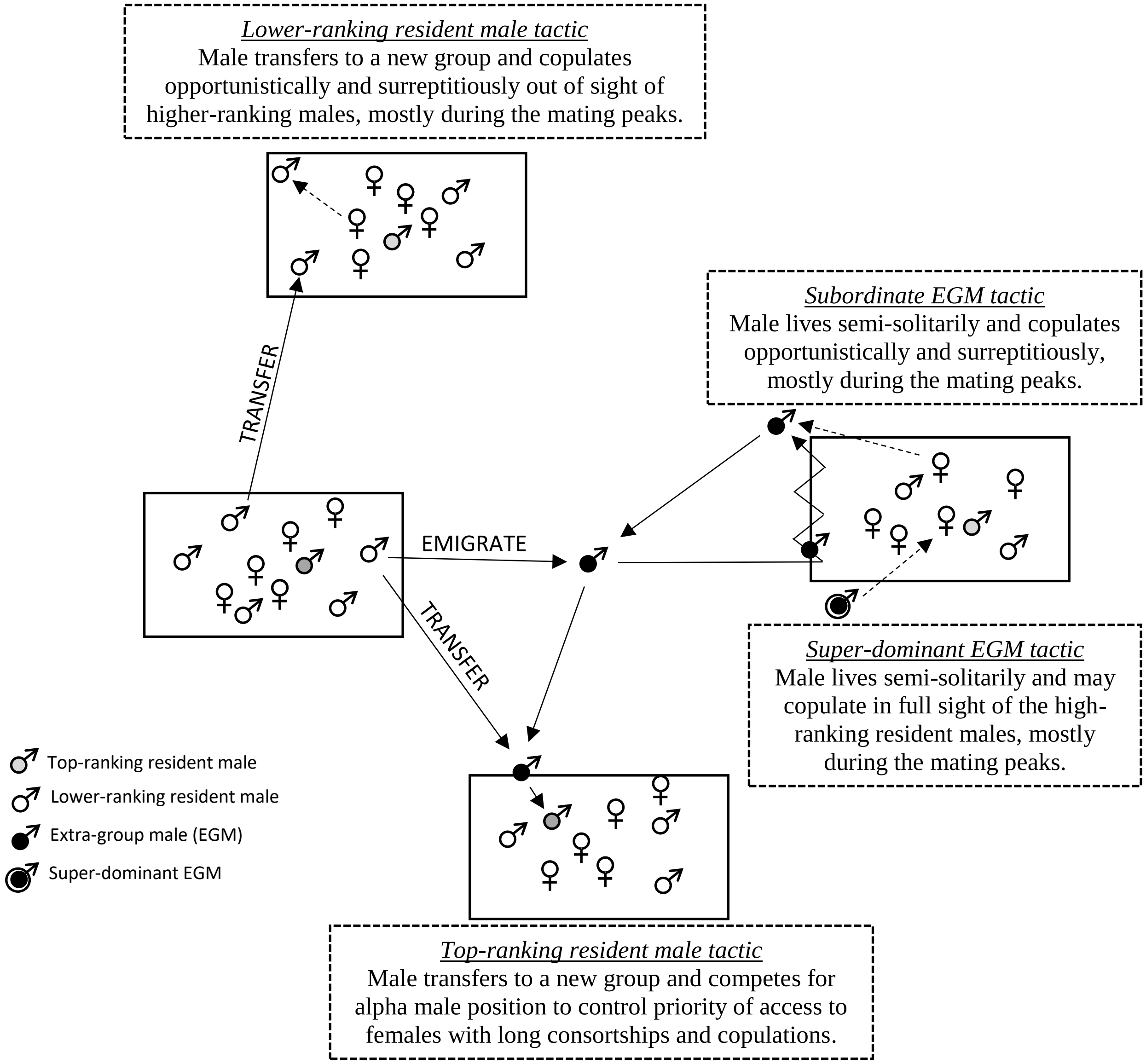
6. Northern pig-tailed macaques would be an interesting candidate for studying multimodal signaling. Both males and females express red coloration in the anogenital area. Both males and females display a wide repertoire of facial expressions (Carlson, 2011; Maestripieri, 2005) and vocalizations during copulations (copulation calls, Carlson, 2011). So far, no studies have reported olfactory signals in northern pig-tailed macaques, but the presence of such signals in other macaque species (e.g., rhesus macaques, Michael & Keverne, 1968; Michael & Zumpe, 1982; stump-tailed macaques, Cerda-Molina, Hernández-López, Rojas-Maya, Murcia-Mejía, & Mondragón-Ceballos, 2006) indicates that captive studies should investigate such signals in northern pig-tailed macaques. Comprehensive studies examining multimodal signals are interesting because we are still lacking knowledge about what information multimodal signals convey to the receivers and whether such signals convey the same information or different

aspects of an individual condition (Higham, Pfefferle, et al., 2013).

7. Long-term studies of behavioral and genetic paternity data in other populations of northern pig-tailed macaques and other moderately seasonally breeding macaques will help to assess the diversity of their mating patterns and the factors (environmental, demographic) that may affect male and female reproductive strategies.

8. To gain a comprehensive picture of male reproductive success, further studies need to look at postcopulatory mechanisms (sperm competition, female cryptic choice), despite the difficulties of conducting such research.

9. Lastly, northern pig-tailed macaques remain poorly studied in the wild (this study; Carlson, 2011; Choudhury, 2008; Feeroz, 2003) and have mostly been studied in one population at Khao Yai National Park (this study; Carlson, 2011). Studies from different populations are necessary to better understand the sexual behaviors and strategies of the species, and continue to improve our understanding of sexual selection and mating strategies among macaque and other primate species.



Lower-ranking resident male tactic
Male transfers to a new group and copulates opportunistically and surreptitiously out of sight of higher-ranking males, mostly during the mating peaks.

Subordinate EGM tactic
Male lives semi-solitarily and copulates opportunistically and surreptitiously, mostly during the mating peaks.

Super-dominant EGM tactic
Male lives semi-solitarily and may copulate in full sight of the high-ranking resident males, mostly during the mating peaks.

Top-ranking resident male tactic
Male transfers to a new group and competes for alpha male position to control priority of access to females with long consortships and copulations.

Figure 7.1 Male mating tactics in northern pig-tailed macaques.

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