The Influence of Genetic and Social Structure on Reproduction in Phayre's Leaf Monkeys (*Trachypithecus phayrei crepusculus*)

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Abstract of the Dissertation

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Dispersal patterns, reproductive skew, and social structure have important fitness consequences for individuals. Intra-sexual competition and kinship have been suggested to directly or indirectly increase inclusive fitness. Thus individual, social, and ecological aspects may shape non-random dispersal and subsequent reproductive success. Primate studies have also shown strong support for the importance of kin interactions on dispersal decisions including contexts favoring an individual to leave to avoid inbreeding or competition and contexts favoring an individual to stay to increase fitness through cooperation. The genetic, ecological and social contexts are particularly important for female primates who also directly influence the growth, maturation, and reproduction of their offspring through nutritional and social maternal effects, particularly in early development.

Phayre's leaf monkeys (*Trachyithecus phayrei crepusculus*) are Asian colobine primates, which are known to exhibit frequent female dispersal, both one- and multi-male groups, linear female dominance hierarchies, and infants that are born with conspicuous natal coats. Thus, this species was ideal to investigate the influence of genetic and social structure on reproduction in a wild population from Phu Khieo Wildlife Sanctuary, Thailand. The study addressed 3 main goals, including: (1) to determine how groups are genetically structured and by what means, (2) to assess what influence, if any, kinship and familiarity have on female dispersal decisions and success at reproducing, and (3) to explore if nutritional and social maternal effects promote infant development following a successful reproduction.

Using genomic DNA extracted from 384 fecal samples collected from 2002-2008, I conducted primer screening on 60 adult individuals from both novel (n=8) and established (n=49) microsatellite loci as well as genetic analyses using 141 individuals across 19 polymorphic loci to explore dispersal patterns, genetic structure and reproductive success. I then combined dispersal and genetic data to explore emigration (n=60) and immigration (n=61) events in relation to age and reproductive status, dyadic relatedness, and successful reproduction between 2001-2009. Data on maternal effects and infant development were collected on two groups from December 2004 through May 2006. I assessed the physical condition of all females, including mothers, monthly (7-point scale, 19 females). Dominance rank (high, medium, low) was based on agonistic interactions and group size was averaged for the study period. To quantify infant development, I recorded the beginning, end, and duration (n=30 measures) in conspicuous natal coat and skin coloration of 13 infants.

In relation to the first goal (Chapter 2), I found a suite of 18 highly variable markers that genotyped consistently and accurately. Allelic diversity ranged from 5-14 alleles per locus, with expected heterozygosities ranging from 0.679-0.884. The high polymorphism and exclusionary power for identifying parentage provided by this panel are useful for examining population structure, dispersal, kinship and reproductive success in the study population and can serve as a useful resource for intra- and interspecific molecular studies on other Asian leaf monkeys. Genetic analyses (Chapter 3) revealed that the population exhibited some structure, gene flow in both sexes, and same-sexed kin both within and between groups. Coupling behavioral data with genetic data reveals that females' likely mediated gene flow through natal and secondary dispersal (sometimes pregnant or with offspring), although males contributed through extra group paternities and may also leave to form new groups.

In relation to the second goal (Chapter 4), female emigration was driven by inbreeding avoidance (to avoid fathers, brothers or maturing sons) for both natal and secondary dispersers in addition to competition among breeding females. While females may enter groups containing female kin, female immigration decisions were most likely influenced by avoidance of familiar kin (males and females) and females are significantly more successful at reproducing in groups with unfamiliar female kin. The results indicate that kin avoidance may also confer fitness benefits, especially in female dispersal species.

In relation to the third goal (Chapter 5), I found variation in female nutritional condition that was improved with rank, although all mother's physical conditions steadily declined after birth. There was also considerable variation in infant development (e.g., total color change differed by 21 weeks) with changes in skin and coat color primarily

depending on nutritional (mother’s nutritional condition) but also social (group size) maternal effects. Thus, results indicate that Phayre’s infants and mothers may benefit from a good maternal nutritional condition (and possibly high rank), positively influencing speed of infant development and potentially growth, which may ultimately increase female reproductive success.

Dedications

I dedicate this dissertation to
my mother, Maureen Larney, and sister, Bridget Scher.
You both continue to be two of my biggest supporters and
the most important people in my life.
Thank you for everything.

Table of Contents

PART I: Introduction

PART II: Molecular methods

PART III: Population Substructure, Dispersal & Reproductive Success

PART IV: Maternal effects on infant development

PART V: Conclusions and future research

List of Figures

List of Tables

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Chapter 1

Introduction and Summary of Chapters

Dispersal Theory

Dispersal patterns, social structure, and individual reproductive success influence genetic variation within and among social groups across space and time (Altmann et al. 1996, Clobert et al. 2001, Gandon and Michalakis 2001, Vigilant et al. 2001, Di Fiore 2009, Lukas and Clutton-Brock 2011). Dispersal affects inbreeding (Roze and Rousset 2003, Gandon 1999, Pusey and Wolf 1996), social relationships (Le Galliard et al. 2005, Silk 2002), an individual's life history (e.g., Pen 2000), and the evolution of species (see review in Barton 2001).

A central goal of dispersal theory, and particularly sex-biases in dispersal, includes understanding both the ultimate (evolutionary) and proximate (immediate mechanistic or social factors) causes of dispersal (Hamilton and May 1977, Pusey and Wolf 1996, Gandon and Michalakis 2001, Lawson Handley and Perrin 2007, Long et al. 2008). Ultimate causes of dispersal include: (1) inbreeding avoidance (Packer 1979, Dobson 1982, Shields 1982, Waser et al. 1986, Pusey 1987, Clutton-Brock 1989, Pusey and Wolf 1996, Gandon 1999, Lukas and Clutton-Brock 2011, Clutton-Brock and Lukas 2012), (2) reducing mate competition (Dobson 1982, Hamilton 1967, Moore and Ali 1984), and (3) reducing competition for resources (Murray 1967, Clarke 1978, Greenwood 1980, 1983, Pusey and Packer 1987, Shields 1987, Bowler and Benton 2005, Ronce et al. 2001). On the other hand, the importance of social relationships (e.g., Silk et al. 2003), group size and with it increased aggression and competition (e.g., Watts 1994,

Pope 2000, Stokes et al. 2003), and intrasexual competition (density dependent increases in aggression; Moore and Ali 1984, Pope 2000, Clobert et al. 2004, Bonenfant et al. 2009) have been described in proximate dispersal decisions. In this regard, genetic relationships are considered fundamental in understanding dispersal decisions (Hamilton 1964, Greenwood 1980, Pusey 1987; Clutton-Brock 1989, Pusey and Wolf 1996, Sterck et al. 1997, Lawson Handley and Perrin 2007). Studies have shown strong support for the effect of kin interactions on dispersal decisions including contexts favoring an individual to stay in the presence of kin potentially increasing inclusive fitness through cooperation (e.g., Hamilton 1964, Wrangham 1980, Sterck et al. 1997) and contexts favoring an individual to leave due to competition (e.g., Hamilton and May 1977, Gandon 1999), particularly in relation to ecological and reproductive constraints (Wrangham 1980, Sterck et al. 1997, Bowler and Benton 2005, Ronce et al. 2001). The latter may lead to avoidance of kin in an attempt to avoid kin competition (Hamilton and May 1977, Gandon 1999, Ronce 2007).

For many taxa, especially birds and mammals, groups exhibit sex-biased dispersal patterns where males and females differ in their age at dispersal, dispersal distance, or other characteristics (for review see Lawson Handley and Perrin 2007). Complete bias in dispersal, where one sex remains exclusively philopatric, is rare in mammals but generally more common in birds and to some degree in primates (Pusey and Packer 1987, Greenwood 1980, Johnson and Gaines 1990, Lawson Handley and Perrin 2007, Lukas and Clutton-Brock 2011). Inbreeding avoidance and the reduction of competition over resources have been suggested to increase the fitness of same-sexed conspecifics often resulting in sex-biases in dispersal (Greenwood 1980, Gandon 1999, Matthysen 2005,

Lawson Handley and Perrin 2007, Gros et al. 2008). For many social mammals and birds, males typically emigrate from their natal group and females remain philopatric, or in their natal group throughout a lifetime (Greenwood 1980, Pusey and Packer 1987). This trend has been widely found in studies of most cercopithecine primates (Wrangham 1980, Melnick and Pearl 1987, Pusey and Packer 1987, Clutton-Brock 2009). However, in several strepsirrhine, platyrrhine, colobine, and hominoid primates, females are the predominant dispersers or both sexes disperse but at varying distances or ages (Moore 1984, Pusey and Packer 1987, Pope 1992, Strier 1994, Nishimura 2003, Stokes et al. 2003, Di Fiore 2003, Bradley et al. 2004, Bradley et al. 2007, Douadi et al. 2007, Huck et al. 2007, Lawson-Handley and Perrin 2007, Morelli et al. 2009, Di Fiore 2009, Di Fiore et al. 2009, Clutton-Brock and Lucas 2012, Yan 2012, Inoue et al. 2013)

Research on female dispersal species has been important in challenging primate socio-ecological models (Wrangham 1980, van Schaik 1989, Sterck et al. 1997) and female dispersal species appear to display more social complexity than previously thought (Moore 1999, but see Clutton-Brock and Lukas 2012); to a point that predictions about dispersal in socio-ecological models have been questioned (Koenig and Borries 2009, Clutton-Brock and Janson 2012). Similar to other social animals, female dispersal in nonhuman primates has commonly been linked to inbreeding avoidance (Moore 1984, Watts 1990, Clutton-Brock 1989, Sterck 1997, Starin 2001, Bradley et al. 2007, Lukas and Clutton-Brock 2011, Clutton-Brock and Lukas 2012), but infanticide avoidance (Crockett and Janson 2000, Stokes et al. 2003, Watts 1990, Sterck 1997, Lukas and Clutton-Brock 2011) and the reduction in scramble competition (e.g., Jones 1980, Wrangham 1980, Glander 1992, Sterck 1997, 1998, Crockett and Janson 2000) has also

been suggested to shape female dispersal decisions. In addition, context dependent strategies often vary for natal versus secondary dispersers (Pusey and Packer 1987, Pope 2000, Starin 2001, Stokes et al. 2003).

Similar to other social animals, genetic relatedness is considered a principle characteristic driving the structure of social groups and suggested to have direct influences on ecological and social contexts in gregarious primates (Wrangham 1980, Isbell 1991, Moore 1992, van Schaik 1989, Sterck et al. 1997). Recent studies have shown how non-random dispersal may result in groups with same-sexed kin (Starin 1994, Watts 1994, Pope 2000, Lukas et al. 2005, Bradley et al. 2007) via cohort dispersal (Starin 1994, Watts 1994, Bradley et al. 2007) or dispersing into groups consisting of related natal females (Starin 1994). In addition, despite initial dispersal, female kin groups can develop over time (Pope 2000) or additional social or anthropogenic factors that may lead to groups disbanding (Stokes et al. 2003, Di Fiore 2009) could result in groups containing female relatives despite female dispersal. This opportunity to overlap with kin despite dispersal could provide the potential for kin-biased behaviors (Chapais 2001, Bradley et al. 2007). Molecular studies have also shown how it is possible that gene flow within a population can still be mediated through the more philopatric sex (Schubert et al. 2011) or dispersal distances may be underrepresented by sampling methodology (Inoue et al. 2013). Patterns of within group genetic relatedness may also be influenced if there is a high reproductive skew among males within social groups, which results in cohorts of similarly aged individuals being more closely related to one another through common paternity than are animals of different ages (e.g., Pope 1990, Widdig et al. 2001, 2002). Similarly, extra-group mating by either males or females can act to

reduce the extent of genetic differentiation between groups (Vigilant et al. 2001, Di Fiore 2009).

However, long-term demographic, social and genetic data on group-living female dispersal species are comparatively rare. Long-term databases for chimpanzees (Pusey 1979, Pusey et al. 1997, Vigilant et al. 2001, Langergraber et al. 2007), bonobos (Kano 1992), gorillas (Harcourt 1978, Stokes et al. 2003, Bradley et al. 2007), hamadryas baboons (Sigg et al. 1982), African colobines (Starin 1994, Korstjens and Schippers 2003, Teichroeb et al. 2009, Wikberg et al. 2012, Minhós et al. 2013), Asian colobines (Poirier 1969, 1970, Rudran 1973, Newton 1987, Kool 1989, Stanford 1991, Sterck 1997, Borries et al. 2004, Yan 2012), Atelids (Symington 1987, Strier 1990, Strier 1994, Crocket and Pope 1993, Ellsworth 2000, Nishimura 2003, Di Fiore and Fleischer 2005, Di Fiore and Campbell 2007, Di Fiore et al. 2009), squirrel monkeys (Mitchell et al. 1991, Blair and Melnick 2012), and lemurs (Morelli et al. 2009) have received more attention. Relatively few studies, however, actually use molecular data to investigate links between female dispersal patterns, kinship, and social behavior (i.e., Hohmann et al. 1999, Pope 2000, Mitani et al. 2002, Stokes et al. 2003, Di Fiore and Fleischer 2005, Langergraber et al. 2007, Morelli et al. 2009, Di Fiore 2009, Di Fiore et al. 2009, Yan 2012). Even fewer explore these variables in relation to either male (Pope 1990, Vigilant et al. 2001, Bradley et al. 2005, Boesch et al. 2006, Langergraber et al. 2007, Inoue et al. 2008, Nsubuga et al. 2008, Inoue et al. 2013) or female (i.e., Pusey et al. 1997, Pope 2000, Stokes et al. 2003) reproductive success.

Kin recognition

A basic assumption of kin selection theory is that individuals have the ability to decipher relatives either through kin recognition or discrimination, which is still debated in the literature (e.g., Blaustein et al. 1991, Chapais et al. 1997, Rendall 2004, Holmes and Mateo 2007). Proper kin recognition allows altruistic acts to be directed to the right recipient and avoid inbreeding. However, while primates are believed to exhibit finely developed kin recognition abilities (Silk 2002), using locational cues for kin recognition is not believed to be effective for gregarious species (Hamilton 1987), such as primates.

In fact, studies of young monkeys found no discrimination among kin and nonkin during interactions when familiarity was held constant (MacKenzie et al. 1985, Sackett and Frederickson 1987, Welker et al. 1987, Erhart et al. 1997, Martin 1997, Widdig et al. 2001). Most research also suggests that since primates rely on familiarity, individuals cannot recognize paternal kin since larger social groups often contain several potential sires and discriminating kin from non-kin would rely on the ability to recognize familial alleles or phenotypic matching (Gouzoules and Gouzoules 1987, Chapais 1995, Mitani et al. 2000). Preliminary studies suggest baboons may decipher individuals that exhibit familial cues (Alberts 1999, Smith 2000) and some evidence shows situation dependent recognition of paternal-kin (Widdig et al. 2001, 2002). However, a criticism of the latter study is that this bias could also result from a preference for age-related cohorts that happened to be sired by a high-ranking male rather than inert recognition (Altmann 1979, Smith et al. 2003, Chapais and Berman 2004, Rendall 2004). Nontheless, there is still little support for the preference of maternal siblings, which should be preferred similarly to paternal kin given equal levels of relatedness (Chapais and Berman 2004). To date, the most support for kin recognition among primates is through the mechanism of familiarity

with individuals during early development (Rendall 2004). Thus, primate studies have shown the most support for familiarity, independent of genetic relatedness, to play an important role in shaping social behaviors in primates

Competition and cooperation among kin and non-kin

Kinship can be a proximate mechanism triggering dispersal to avoid inbreeding or kin competition (Pusey and Wolf 1996, Ronce et al. 2001) or as a means to formulate affiliative and cooperative relationships with relatives. According to Hamilton's rule, selection will depend on the balance between the inclusive fitness benefits of the trait and the direct fitness costs to the individual (Hamilton 1964). Competiton is at the core of many theoretical and empirical studies of dispersal (Lambin et al. 2001), yet theory has shown early on that such ecological benefits are not a necessary requirement for dispersal to evolve as a strategy for avoiding kin-competition in stable habitats (Hamilton and May 1977). Rather, the evolution of dispersal could be viewed as an altruistic behavior, providing no direct ecological benefit to the dispersed individual, but alleviating competition with its kin (Hamilton and May 1977, Ronce 2007). Assuming that interactions between kin have the same direct fitness costs as interactions between non-kin, dispersal may result in siblings competing with nonsiblings at many sites instead of parents and offspring or siblings competing with themselves at a natal site (Hamilton and May 1977, Ronce et al. 2001). For some animals, the presence of kin within a patch may positively influence fitness, for instance through cooperative behavior. When dispersal is costly, dispersal may be selected against and provide the environment for the evolution of cooperative behavior which may be aided by kin selection (Hamilton 1964). Kin-biased

behaviors can increase inclusive fitness either directly or indirecty (Hamilton 1964). Kin selection has been widely accepted as a major factor shaping primate affiliative and cooperative behavior (Chapais 2001, Chapais and Belisle 2004, Silk 2002, 2007), especially in several ceropithecine primates (Gouzoules 1984, Gouzoules and Gouzoules 1987, Walters 1987, Silk 2002, Chapais 2006) but also some great apes (Watts 1994, Stewart and Harcourt 1987) and new world monkeys (Perry et al. 2008, Pope 1990, 2000). Female kin alliances have been primarily suggested to help gain access to food resources (Wrangham 1980, van Schaik 1989, Sterck et al. 1997) and research has suggested that this can have a positive influence on food intake (Koenig 2002). Female kin associations have been shown to improve female reproductive success, infant survival, longevity and, ultimately, fitness (Pope 1990, 2000, Silk 2002, Silk et al. 2003, 2009, 2010).

Even among the dispersing sex, same-sex matrilines or patrilines can develop over time if dispersal is a condition dependent tactic and there are benefits to cooperating with same-sexed kin for either ecological (Wrangham 1980, Sterck et al. 1997) or reproductive (e.g., Pope 1990, 2000) resources. However, living in a group does not necessarily mean living with kin, even for the pilopatric sex (Moore 1992, Lukas et al. 2005) and more importantly, having same-sexed kin in a social group does not necessarily translate into a bias towards nepotistic affiliative or cooperative behaviors (e.g., Seyfarth and Cheney 1984, Muroyama 1994, Henzi and Barrett 1999, Silk et al. 1999, Barrett et al. 2000, Mitani et al. 2002, Boesch et al. 2006, Langergraber et al. 2007). In fact, primate studies are providing more support for the prevelance and imporatance of non- or distantly related kin associations with individuals of similar age

or rank rather than with both maternal (Hashimoto et al. 1996, Mitani et al. 2002, Langergraber et al. 2007) or paternal (Langergraber et al. 2007) relatives. Thus, affiliation with non-kin is prevalent in many primates and may be more influential in some primate societies than kin-selection (Silk 2002, Chapais 2006, Langergraber et al. 2007). Reciprocity, regardless of kinship, may result in important benefits (Trivers 1971, Noë 2001) and other individual and social factors (e.g., group size, rank) should be considered as equally important variables for reproductive success and in both males and females.

Maternal effects on reproduction and development

In fact, mammalian life histories are influenced by genetic, demographic, ecological and social factors. Fitness is primarily dependent on an individual's genetic contribution into subsequent generations through offspring survival (Clutton-Brock 1988). In turn, offspring survival depends on their phenotype, which, in addition to genetic factors, can be affected by parental non-genetic factors such as maternal effects (overviews in Kirkpatrick and Lande 1989, Bernardo 1996, Mousseau and Fox 1998, Maestripieri and Mateo 2009). Maternal effects may influence offspring fitness in various ways, primarily through nutrition, behavioral or physiological mechanisms, or social effects such as group size or dominance rank (see summary in Maestripieri and Mateo 2009).

Female mammals invest substantially in both their pre- and postnatal contribution to offspring and maternal nutritional effects are suggested to have a particularly strong influence on infant development and survival in various mammals (Côté and Festa-

Bianchet 2001, Altmann and Alberts 2005, Gendreau et al. 2005, Vervaecke et al. 2005). Thus, access to resources is of prime importance in terms of female reproductive success in mammals (Wrangham 1980, van Schaik 1989), because levels of body fat affect ovulation, likelihood of conception, successful pregnancy and the ability to lactate (Koenig et al. 1997, McFarland 1997, Ellison 2003). In addition, it has been shown that a mother's nutritional condition influences the amount of milk yield, where females in better nutritional conditions produce a larger volume of milk compared to females in poorer condition (Landete-Castillejos et al. 2005, Hinde et al. 2009). Enhanced milk production has also been associated with accelerated infant development (Hinde 2007, Hinde et al. 2009).

Maternal nutritional effects among mammals have been dominated by studies of rodents and ungulates, while mammals with long life histories, such as nonhuman primates (Charnov and Berrigan 1993, Kappeler and Pereira 2003), have been underrepresented (see summary in Maestripieri and Mateo 2009). In nonhuman primates, offspring are born in an altricial state and tend to have slow growth rates compared to other mammals (Charnov and Berrigan 1993, Kappeler and Pereira 2003). This leads to considerable dependency of infants in the first years of life and a substantial burden on the mother through lactation (Altmann 1980, Lee 1987). Although nutritional requirements vary among mammals (overview in Tardif et al. 2001), this dependency is particularly crucial for survival through the first weeks of a primate infant's life since an older infant can supplement its mother's milk with foraging and ingesting foods independently. Consequently, nonhuman primates would make very suitable subjects for the study of maternal effects. However, both measures of maternal nutritional condition

and effects on infant growth and development are difficult to obtain for arboreal animals, including most primates, because the individuals are more difficult to observe.

In contrast, social maternal effects have been studied in some detail in terrestrial nonhuman primates such as baboons (Altamann 1980, Altmann and Alberts 2005). Among other aspects such as sex ratio adjustment or maternal effects on behavior (see overview in Maestripieri and Mateo 2009), it has been found that differences in dominance rank of mothers might be associated with substantial variation in offspring growth (e.g., Johnson 2003, Altmann and Alberts 2005). More generally, high rank of a mother may confer reproductive advantages in terms of shorter interbirth intervals or higher birth rates, likely indicating faster growth (Pusey et al. 1997, van Noordwijk and van Schaik 1999, Altmann and Alberts 2003). However, maternal rank effects on reproductive success have not always been found (see overview in Stockley and Bro-Jørgensen 2011). In theory, females may establish dominance relationships and gain better access to food if resources can be monopolized (Janson and van Schaik 1988, overview in Koenig 2002). Under these conditions, one expects females of high rank to gain more energy (Janson 1985, Vogel 2005) and therefore be in better nutritional condition (Koenig 2000). Thus, whether dominance rank indeed confers the predicted effects on offspring growth and reproductive success depends on an actual association of rank with energy gain and maternal nutritional condition, an association that has rarely been tested, especially in arboreal primates.

However, maternal condition may not be solely rank dependent and affected by direct competition over food, but may also depend on indirect (or scramble) competition (Janson and van Schaik 1988, van Schaik 1989, Giraldeau and Caraco 2000). As group

size (or density) increases, limiting food resources will be depleted faster, forcing individuals to increase foraging effort (Pyke 1984, Janson and van Schaik 1988, Chapman and Chapman 2000). As a result, individuals in large groups may be characterized by lower energy gain, which ultimately may lead to poorer maternal condition, slower growth, and reduced reproductive rates (Janson and van Schaik 1988, van Schaik 1989). While group size or density dependent effects on foraging effort or reproductive rate are well-known for nonhuman primates (van Noordwijk and van Schaik 1999, Altmann and Alberts 2005, Borries et al. 2008), the actual effects of maternal nutritional condition on infant development and growth are virtually unstudied (but see Altmann and Alberts 2005).

What is known about colobines?

For a number of reasons, Asian colobines provide a good model to investigate the influence of genetic and social structure on reproduction in a wild population. Colobines are best known for their specialized dietary adaptations for digesting leaves, and diets typically contain a relatively large proportion of leaves, but also fruits, seeds and occasionally flowers, animal byproducts and terrestrial vegetation or lichens (Koenig and Borries 2001, Fashing 2007, Kirkpatrick 2007, Sterck 2012). Colobines are generally described as arboreal primates with most species characterized by both male and female dispersal. They live in rather small groups, with polygynous one-male, multi-female groups and/ or promiscuous multi-male, multi-female units the norm and social relationships are generally described as rather tolerant. In terms of life history, colobines are generally assumed to be on the fast end of the "fast-slow continuum", although

contradictory patterns in growth and development suggest that this categorization may be overly simplified (see below; Struhsaker 1975, Struhsaker and Leland 1987, Koenig and Borries 2001, Korstjens and Noe 2004, Arnold and Aureli 2007, Leigh et al. 2007, Kirkpatrick 2011, Sterck 2012).

Variability in dispersal patterns

To date, studies on dispersal in colobines have have focused on females due to the simple fact that female dispersal is so common in this subfamily. As a consequence, patterns and explanations for male dispersal strategies are typically underrepresented. Conflicting patterns of dispersal have been suggested for male colobines, with review papers generally describing males as the dispersing (Kirkpatrick 2011) or philopatric (Sterck 2012) sex. This disparity may be, in part, due to the extensive variability in colobines with some species characterized by male dispersal and female philopatry (Proboscis monkey, Boonratana 1999; guereza, Harris et al. 2009; Hanuman langur, Borries 2000, Koenig 2000, Koenig and Borries 2001; Nilgiri langurs, banded leaf-monkeys, purple-faced langurs, red leaf monkeys and guereza, Newton and Dunbar 1994), others by female dispersal and male philopatry (red colobus, Struhsaker and Leland 1979, Starin 1994), and still others by bisexual dispersal (olive colobus, Korstjens and Schippers 2003; Thomas's leaf monkey, Sterck et al. 2005; ursine colobus, Saj et al. 2007, Teichroeb and Sicotte 2009, Wikberg et al. 2012; golden snub-nosed monkeys, Zhao et al. 2008a, Yao et al. 2011, Yan 2012). However, few colobine studies have succeeded in combining observational and molecular data in describing dispersal patterns (but see *Colobus guereza*, Harris et al. 2009; *Colobus vellerosus*, Teichroeb et al. 2009,

Teichroeb and Sicotte 2011, Wikberg et al. 2012), particularly for Asian species (but see golden snub-nosed monkeys, Zhao et al. 2008a, Yan 2012).

Males should immigrate to increase mating opportunities, search for groups with a more favorable adult male/ adult female ratio, and to obtain higher rank. However, most of our knowledge on dispersal in colobine males comes from Hanuman langurs, which show a range of male options that are closely related to age, dominance, and seasonality in mating (Borries 2000). Reports of solitary males and all-male bands are common, and typically result from three circumstances: (1) aggressive eviction from natal groups (Hanuman langur, Treves and Chapman 1996; ursine colobus, Teichroeb and Sicotte 2011), voluntarily leaving previous groups (capped leaf monkeys, Stanford 1991b; ursine colobus, Teichroeb and Sicotte 2011), or being left by ther mothers (with male residents) following female secondary dispersal (Thomas's leaf monkey, Steenbeek et al. 2000). Solitary males may take over groups aggressively (Hanuman langur, Sugiyama 1965, Borries 2000; guereza, Struhsaker and Leland 1979; ursine colobus, Teichroeb and Sicotte 2011) or by attracting females and forming new groups (Marsh 1979b, Stanford 1991b, Sterck 1997, Sterck 2012). All-male bands may form due to predation risk and have also been observed to form coalitions to take over groups (Rajpurohit and Sommer 1993). While subordinate males may gain some mating opportunities or inclusive fitness benefits by remaining in a group with other males, all males should attempt to gain alpha positions, as rank and mating success is likely correlated (Borries 2000). Thus, decisions on whether to remain in or leave a group is likely dependent on age and if a young male in his prime doesn't achieve alpha position, he should emigrate. The dominant male should hold his positon for as long as he can and new males may attempt to force other

young males to leave (Rajpurohit and Sommer 1993, Borries 2000). Older males, however, may remain or disperse as long as they can gain some access to cycling females (Borries 2000).

Female transfer in colobines is common, particularly in Asian colobines (Yeager and Kool 2000, Sterck and van Hooff 2000), although the age and reproductive status of dispersing females may vary. While several colobine populations have only observed cases of natal dispersal by nulliparous females (red colobus, Struhsaker and Leland 1979), others have extensively documented both natal and secondarily dispersal (red colobus, Marsh 1979a,b; capped leaf monkeys, Stanford 1991b, Thomas's leaf monkey, Sterck et al. 2005; golden snub-nosed monkey, Zhao et al. 2008a; ursine colobus, Teichroeb et al. 2009). Natal dispersal is mainly suggested as a mechanism of inbreeding avoidance (Sterck and Korstjens 2000; olive colobus, Korstjens and Schippers 2003; golden snub-nosed monkey, Zhao et al. 2008a; but see ursine colobus, Teichroeb et al. 2009). Secondary dispersal seems to be a female strategy to avoid infanticide in some species. By transferring into smaller groups where infants might be less of a target (Hanuman langur, Treves and Chapman 1996; Thomas's leaf monkey, Steenbeek and van Schaik 2001), and leaving groups when extragroup males challenge resident males (Thomas's leaf monkey, Sterck 1997) or male group membership is unstable (ursine colobus, Teichroeb et al. 2009), females reduce the risk of infanticide. It has also been suggested that females join males who are better protectors against infanticide, and some evidence supports higher infant survival to infants born after dispersals than those born prior to dispersal (with the original males; Thomas's leaf monkey, Sterck et al. 2005). Females may also disperse to reduce competition over resources by transferring to groups

that are similar or smaller in size than their groups of origin (Thomas's leaf monkey, Sterck 1997; olive colobus, Korstjens and Schippers 2003; golden snub-nosed monkey, Zhao et al. 2008a; ursine colobus, Teichroeb et al. 2009).

Female dispersal can be voluntary (Thomas's leaf monkey, Sterck 1997) or forced when females are evicted from their group (king colobus, Korstjens et al. 2002; reviewed in Sterck and Korstjens 2000). Researchers rarely report solitary dispersing females ranging alone. While this may be an artifact of missed observations due to shy animals, it has also been suggested that female colobines disperse socially, joining adjacent social groups whose ranges overlap extensively with their own, strategically moving directly from one group into another (Isbell and van Vuren 1996). Females have also been observed to display parallel dispersal via same-sexed cohorts (e.g., red colobus, Starin 1991) or by following members of other species (e.g., olive colobus, Korstjens and Schippers 2003). And females may often join groups with familiar individuals and kin (Sterck et al. 2005, Teichroeb et al. 2009) or form new groups within their natal home range (Isbell and van Vuren 1996). Females may emigrate to follow and join (a) lone male(s) or transfer to a small, newly formed group (capped leaf monkey, Stanford 1991c; Thomas's leaf monkey, Steenbeek et al. 2000). In some species, however, dispersing females have been reported to disperse at large distances into entirely new home ranges (e.g., red colobus, Marsh 1979a, Starin 1994; olive colobus, Korstjens and Schippers 2003).

In some species, resident females may try to prevent immigrating females through directed aggression (ursine colobus, Teichroeb et al. 2009), while other species are typically more welcoming (Sterck et al. 2005, Sterck 2012). Female transfer between

existing groups may be a means of evaluating both females as well as male characteristics (Kirckpatrick 2011). It has been suggested that dispersing females with infants may be especially vulnerable to predation and infanticide by new males and typically disperse without dependent offspring (Sterck and Korstjens 2000). However, females may also transfer with dependent offspring (*T. johnii*, Poirier 1970; *P. siamensis*, Bennett 1983; *N. larvatus*, Bennett and Sebastian 1988), suggesting that infanticide risk in some species may be low.

Group composition and dynamics

Most colobines live in one-male, multiple-female groups (Moore 1999, Kirkpatrick 2011, Sterck 2012), where a single male is able to monopolize several females and sires most, if not all, offspring (Launhardt et al. 2001). Some colobines, however, consist of both one and multi-male groups (*Procolobus, Nasalis, Rhinopithecus,* some *Colobus, Trachypithecus* and *Semnopithecus*), which has been suggested to result from the maturation of natal males (Sterck and van Hooff 2000; Koenig and Borries 2012) or male immigration (Moore 1999, Borries and Koenig 2000). Some males are observed to join one-male groups with little aggression (Nilgiri langur, Poirier 1970; banded leaf monkey, Hohmann 1989, Megantara 1989). However, multi-male groups develop clear dominance hierarchies and alpha males have preferential mating access to females, but cannot always monopolize all females (red colobus, Struhsaker and Leland 1979, Struhsaker and Pope 1991, Starin 1994, Hanuman langurs: Borries and Koenig 2000, Launhardt et al. 2001; guereza, Harris and Monfort 2003). Group size in both one- and multi-male groups is surprisingly similar, although both vary and can include up to

15 adult females (Newton 1987, Sterck and van Hooff 2000, Kirkpatrick 2011). While some multi-male groups are stable over time, many are suggested to be transitional. Intra-group male contests can be sudden or gradual, but often result in one-male groups; where a resident male is either replaced by a maturing son or a new male (Kirkpatrick 2011). Natal multi-male groups often become age-graded (Thomas's leaf monkey, Steenbeek et al. 2000) and young adult males rarely replace their fathers as the sexually active male (Gurmaya 1986, Steenbeek et al. 2000) and often split, resulting in one-male groups (Nilgiri langur, Hohmann 1989). Most knowledge on stable multi-male groups comes from Hanuman langurs, where there are up to 5 adult males in the group, and males form dominance hierarchies that determine access to receptive females (Borries et al. 1999a). Immigrant males are often former residents of adjacent groups (Borries et al. 1999b) and while they may achieve all ranks, low rank may promote some males to transfer (Borries 2000). Thus, in addition to births and deaths, group changes in colobines appear to be driven by reproductive strategies, including both male competition and female choice. While males compete for access to females, females can choose to either remain or transfer (Kirkpatrick 2011). Intergroup relations appear to be mediated by both males and females and are not necessarily based solely on food defense (resource defense polygyny; Thomas's leaf monkey, Wich et al. 2002 a,b; guereza, Fashing 2001, Harris 2006). Intergroup encounters may facilitate female transfer (e.g., snub-nosed monkeys, Kirkpatrick 1998) and male-male aggression between groups or against new males serves to defend females (female defense polygyny), which has been observed in several colobine species (capped leaf monkey, Stanford 1991a; Thomas's leaf monkey,

Steenbeek et al. 2000, Wich et al. 2002b, Wich and Sterck 2007; king colobus, Korstjens et al. 2002)

Dominance interactions

Despite earlier suggestions (Wrangham 1980, Sterck et al. 1997), recent studies suggest that female colobines compete over food resources, have agonistic relationships, and display despotic dominance hierarchies (Hanuman langurs, Hrdy and Hrdy 1976, Borries et al. 1991, Borries 1993, Koenig 2000, Lu et al. 2008; Thomas's leaf monkey, Sterck and Steenbeek 1997; king colobus, Korstjens et al. 2002; Phayre's leaf monkey, Koenig et al. 2004a). However, unlike stable matrilineal hierarchies in cercopithecine females, dominance hierarchies are often individualistic (not based on kinship or coalition formation) and (inversely) age-graded, with frequent ranks changes (Hanuman, Borries et al. 1991; Phayre's leaf monkeys, Koenig et al. 2004a; guereza, Dunbar and Dunbar 1976; Hanuman langur, Borries 1993, Borries et al. 1991, Koenig 2000; king colobus, Korstjens et al. 2002; ursine colobus, Saj et al. 2007). There is also evidence linking dominance rank to access to food and female fitness. High-ranking female Hanuman langurs are in better body condition (Koenig 2000), ingest more food (Borries 1993), conceive earlier (Koenig et al. 1997), and more often (Borries et al. 1991) compared to low-ranking females. Observations of Thomas's leaf monkeys, on the other hand, have failed to show any influence of female dominance rank on time spent feeding, feeding intake, or reproductive success (Sterck 1995, Sterck et al. 1997). Thus, further studies exploring the impact of female dominance relationships on nutritional condition and reproduction are needed.

Life history

Colobine life history has generally been reported as “fast”, with females giving birth at a younger age, having more offspring over the lifespan, and living shorter lives compared to frugivorous primates of similar body size (Leigh 1994, Wich et al. 2007). However, recent studies have called this idea into question suggesting that colobines might have aspects of life history that are slower (e.g., gestation) compared to cercopithecines (Borries et al. 2011).

Colobine life histories are also influenced by nutritional factors. For instance, provisioning or food abundance are known accelerate age at first reproduction (reviewed in Sterck 2012), increase the probability of conception (e.g., *Rhinopithecus bieti*, Xiang and Sayers 2009; *Semnopithecus entellus*, Koenig et al. 1997; *Trachypithecus leucocephalus*, Jin et al. 2009; *T. phayrei*, Borries and Koenig 2005, reviewed in Brockman and van Schaik 2005), reduce the length of interbirth intervals (e.g., Borries et al. 2001; reviewed in Sterck 2012), and accelerate weaning (white-headed black leaf monkey, Zhao et al. 2008b; silver leaf monkey, Shelmidine et al. 2009). In Hanuman langurs, the pace of life history, as measured by the frequency of births (IBI), is also influenced by social rank, an unsurprising result, given the association between rank and food intake / body condition.

Natal coloration

An interesting aspect of colobines that has received widespread attention is the fact that colobine infants are typically born with natal coloration that changes over the

first months of life (Treves 1997). Natal coats are found in all but one species of colobine (*N. narvatus*, Newton and Dunbar 1994). Most are conspicuous in color and mainly suggested to have evolved to attract female caretakers (infant handling or alloparenting, Hrdy 1976, but see Newton and Dunbar 1994, Treves 1997). Non-maternal caretakers (alloparents) are virtually ubiquitous in colobine monkeys, but there are some exceptions (e.g., red colobus, olive colobus; McKenna 1979; Newton and Dunbar 1994). In fact, red and olive colobus are believed to have darker natal coats due the lack of infant handling. However, the darker coat in Hanuman infants is more likely attributed to camouflage due to the high risks of predation and infanticide (Newton and Dunbar 1994). Infant handling is typical for females, and males may be more tolerant of infants but will alloparent on occasion and more often protect infants (Whitten 1987, Borries et al. 1999b; Kirkpatrick 2011, Sterck 2012). Nonetheless, in addition to improving maternal reproduction, allomothering may have important fitness benefits and costs for mothers, allomothers, and infants (Stanford 1992, Mitani and Watts 1997).

However, less is known about the direct relationship between maternal nutrition, energy transfer via lactation, and early infant development. It remains unclear whether speed of natal color change is a direct consequence of differences in the amount and quality of milk and whether this correlates with body mass of infants. However, several studies strongly support an effect of maternal body mass or fatness on growth rates of infants in both captive as well as wild populations of primates and other mammals (Johnson 2003, Altmann and Alberts 2005, Vervaecke et al. 2005, Hinde et al. 2009, Landete-Castillejos et al. 2010). Thus, it is likely that there are developmental implications for skin and pelage variables (Sumner and Mollon 2003, Bradley and

Chapter 1

Introduction and Summary of Chapters

Dispersal Theory

Dispersal patterns, social structure, and individual reproductive success influence genetic variation within and among social groups across space and time (Altmann et al. 1996, Clobert et al. 2001, Gandon and Michalakis 2001, Vigilant et al. 2001, Di Fiore 2009, Lukas and Clutton-Brock 2011). Dispersal affects inbreeding (Roze and Rousset 2003, Gandon 1999, Pusey and Wolf 1996), social relationships (Le Galliard et al. 2005, Silk 2002), an individual's life history (e.g., Pen 2000), and the evolution of species (see review in Barton 2001).

A central goal of dispersal theory, and particularly sex-biases in dispersal, includes understanding both the ultimate (evolutionary) and proximate (immediate mechanistic or social factors) causes of dispersal (Hamilton and May 1977, Pusey and Wolf 1996, Gandon and Michalakis 2001, Lawson Handley and Perrin 2007, Long et al. 2008). Ultimate causes of dispersal include: (1) inbreeding avoidance (Packer 1979, Dobson 1982, Shields 1982, Waser et al. 1986, Pusey 1987, Clutton-Brock 1989, Pusey and Wolf 1996, Gandon 1999, Lukas and Clutton-Brock 2011, Clutton-Brock and Lukas 2012), (2) reducing mate competition (Dobson 1982, Hamilton 1967, Moore and Ali 1984), and (3) reducing competition for resources (Murray 1967, Clarke 1978, Greenwood 1980, 1983, Pusey and Packer 1987, Shields 1987, Bowler and Benton 2005, Ronce et al. 2001). On the other hand, the importance of social relationships (e.g., Silk et al. 2003), group size and with it increased aggression and competition (e.g., Watts 1994,

Pope 2000, Stokes et al. 2003), and intrasexual competition (density dependent increases in aggression; Moore and Ali 1984, Pope 2000, Clobert et al. 2004, Bonenfant et al. 2009) have been described in proximate dispersal decisions. In this regard, genetic relationships are considered fundamental in understanding dispersal decisions (Hamilton 1964, Greenwood 1980, Pusey 1987; Clutton-Brock 1989, Pusey and Wolf 1996, Sterck et al. 1997, Lawson Handley and Perrin 2007). Studies have shown strong support for the effect of kin interactions on dispersal decisions including contexts favoring an individual to stay in the presence of kin potentially increasing inclusive fitness through cooperation (e.g., Hamilton 1964, Wrangham 1980, Sterck et al. 1997) and contexts favoring an individual to leave due to competition (e.g., Hamilton and May 1977, Gandon 1999), particularly in relation to ecological and reproductive constraints (Wrangham 1980, Sterck et al. 1997, Bowler and Benton 2005, Ronce et al. 2001). The latter may lead to avoidance of kin in an attempt to avoid kin competition (Hamilton and May 1977, Gandon 1999, Ronce 2007).

For many taxa, especially birds and mammals, groups exhibit sex-biased dispersal patterns where males and females differ in their age at dispersal, dispersal distance, or other characteristics (for review see Lawson Handley and Perrin 2007). Complete bias in dispersal, where one sex remains exclusively philopatric, is rare in mammals but generally more common in birds and to some degree in primates (Pusey and Packer 1987, Greenwood 1980, Johnson and Gaines 1990, Lawson Handley and Perrin 2007, Lukas and Clutton-Brock 2011). Inbreeding avoidance and the reduction of competition over resources have been suggested to increase the fitness of same-sexed conspecifics often resulting in sex-biases in dispersal (Greenwood 1980, Gandon 1999, Matthysen 2005,

Lawson Handley and Perrin 2007, Gros et al. 2008). For many social mammals and birds, males typically emigrate from their natal group and females remain philopatric, or in their natal group throughout a lifetime (Greenwood 1980, Pusey and Packer 1987). This trend has been widely found in studies of most cercopithecine primates (Wrangham 1980, Melnick and Pearl 1987, Pusey and Packer 1987, Clutton-Brock 2009). However, in several strepsirrhine, platyrrhine, colobine, and hominoid primates, females are the predominant dispersers or both sexes disperse but at varying distances or ages (Moore 1984, Pusey and Packer 1987, Pope 1992, Strier 1994, Nishimura 2003, Stokes et al. 2003, Di Fiore 2003, Bradley et al. 2004, Bradley et al. 2007, Douadi et al. 2007, Huck et al. 2007, Lawson-Handley and Perrin 2007, Morelli et al. 2009, Di Fiore 2009, Di Fiore et al. 2009, Clutton-Brock and Lucas 2012, Yan 2012, Inoue et al. 2013)

Research on female dispersal species has been important in challenging primate socio-ecological models (Wrangham 1980, van Schaik 1989, Sterck et al. 1997) and female dispersal species appear to display more social complexity than previously thought (Moore 1999, but see Clutton-Brock and Lukas 2012); to a point that predictions about dispersal in socio-ecological models have been questioned (Koenig and Borries 2009, Clutton-Brock and Janson 2012). Similar to other social animals, female dispersal in nonhuman primates has commonly been linked to inbreeding avoidance (Moore 1984, Watts 1990, Clutton-Brock 1989, Sterck 1997, Starin 2001, Bradley et al. 2007, Lukas and Clutton-Brock 2011, Clutton-Brock and Lukas 2012), but infanticide avoidance (Crockett and Janson 2000, Stokes et al. 2003, Watts 1990, Sterck 1997, Lukas and Clutton-Brock 2011) and the reduction in scramble competition (e.g., Jones 1980, Wrangham 1980, Glander 1992, Sterck 1997, 1998, Crockett and Janson 2000) has also

been suggested to shape female dispersal decisions. In addition, context dependent strategies often vary for natal versus secondary dispersers (Pusey and Packer 1987, Pope 2000, Starin 2001, Stokes et al. 2003).

Similar to other social animals, genetic relatedness is considered a principle characteristic driving the structure of social groups and suggested to have direct influences on ecological and social contexts in gregarious primates (Wrangham 1980, Isbell 1991, Moore 1992, van Schaik 1989, Sterck et al. 1997). Recent studies have shown how non-random dispersal may result in groups with same-sexed kin (Starin 1994, Watts 1994, Pope 2000, Lukas et al. 2005, Bradley et al. 2007) via cohort dispersal (Starin 1994, Watts 1994, Bradley et al. 2007) or dispersing into groups consisting of related natal females (Starin 1994). In addition, despite initial dispersal, female kin groups can develop over time (Pope 2000) or additional social or anthropogenic factors that may lead to groups disbanding (Stokes et al. 2003, Di Fiore 2009) could result in groups containing female relatives despite female dispersal. This opportunity to overlap with kin despite dispersal could provide the potential for kin-biased behaviors (Chapais 2001, Bradley et al. 2007). Molecular studies have also shown how it is possible that gene flow within a population can still be mediated through the more philopatric sex (Schubert et al. 2011) or dispersal distances may be underrepresented by sampling methodology (Inoue et al. 2013). Patterns of within group genetic relatedness may also be influenced if there is a high reproductive skew among males within social groups, which results in cohorts of similarly aged individuals being more closely related to one another through common paternity than are animals of different ages (e.g., Pope 1990, Widdig et al. 2001, 2002). Similarly, extra-group mating by either males or females can act to

reduce the extent of genetic differentiation between groups (Vigilant et al. 2001, Di Fiore 2009).

However, long-term demographic, social and genetic data on group-living female dispersal species are comparatively rare. Long-term databases for chimpanzees (Pusey 1979, Pusey et al. 1997, Vigilant et al. 2001, Langergraber et al. 2007), bonobos (Kano 1992), gorillas (Harcourt 1978, Stokes et al. 2003, Bradley et al. 2007), hamadryas baboons (Sigg et al. 1982), African colobines (Starin 1994, Korstjens and Schippers 2003, Teichroeb et al. 2009, Wikberg et al. 2012, Minhós et al. 2013), Asian colobines (Poirier 1969, 1970, Rudran 1973, Newton 1987, Kool 1989, Stanford 1991, Sterck 1997, Borries et al. 2004, Yan 2012), Atelids (Symington 1987, Strier 1990, Strier 1994, Crocket and Pope 1993, Ellsworth 2000, Nishimura 2003, Di Fiore and Fleischer 2005, Di Fiore and Campbell 2007, Di Fiore et al. 2009), squirrel monkeys (Mitchell et al. 1991, Blair and Melnick 2012), and lemurs (Morelli et al. 2009) have received more attention. Relatively few studies, however, actually use molecular data to investigate links between female dispersal patterns, kinship, and social behavior (i.e., Hohmann et al. 1999, Pope 2000, Mitani et al. 2002, Stokes et al. 2003, Di Fiore and Fleischer 2005, Langergraber et al. 2007, Morelli et al. 2009, Di Fiore 2009, Di Fiore et al. 2009, Yan 2012). Even fewer explore these variables in relation to either male (Pope 1990, Vigilant et al. 2001, Bradley et al. 2005, Boesch et al. 2006, Langergraber et al. 2007, Inoue et al. 2008, Nsubuga et al. 2008, Inoue et al. 2013) or female (i.e., Pusey et al. 1997, Pope 2000, Stokes et al. 2003) reproductive success.

Kin recognition

A basic assumption of kin selection theory is that individuals have the ability to decipher relatives either through kin recognition or discrimination, which is still debated in the literature (e.g., Blaustein et al. 1991, Chapais et al. 1997, Rendall 2004, Holmes and Mateo 2007). Proper kin recognition allows altruistic acts to be directed to the right recipient and avoid inbreeding. However, while primates are believed to exhibit finely developed kin recognition abilities (Silk 2002), using locational cues for kin recognition is not believed to be effective for gregarious species (Hamilton 1987), such as primates.

In fact, studies of young monkeys found no discrimination among kin and nonkin during interactions when familiarity was held constant (MacKenzie et al. 1985, Sackett and Frederickson 1987, Welker et al. 1987, Erhart et al. 1997, Martin 1997, Widdig et al. 2001). Most research also suggests that since primates rely on familiarity, individuals cannot recognize paternal kin since larger social groups often contain several potential sires and discriminating kin from non-kin would rely on the ability to recognize familial alleles or phenotypic matching (Gouzoules and Gouzoules 1987, Chapais 1995, Mitani et al. 2000). Preliminary studies suggest baboons may decipher individuals that exhibit familial cues (Alberts 1999, Smith 2000) and some evidence shows situation dependent recognition of paternal-kin (Widdig et al. 2001, 2002). However, a criticism of the latter study is that this bias could also result from a preference for age-related cohorts that happened to be sired by a high-ranking male rather than inert recognition (Altmann 1979, Smith et al. 2003, Chapais and Berman 2004, Rendall 2004). Nontheless, there is still little support for the preference of maternal siblings, which should be preferred similarly to paternal kin given equal levels of relatedness (Chapais and Berman 2004). To date, the most support for kin recognition among primates is through the mechanism of familiarity

with individuals during early development (Rendall 2004). Thus, primate studies have shown the most support for familiarity, independent of genetic relatedness, to play an important role in shaping social behaviors in primates

Competition and cooperation among kin and non-kin

Kinship can be a proximate mechanism triggering dispersal to avoid inbreeding or kin competition (Pusey and Wolf 1996, Ronce et al. 2001) or as a means to formulate affiliative and cooperative relationships with relatives. According to Hamilton's rule, selection will depend on the balance between the inclusive fitness benefits of the trait and the direct fitness costs to the individual (Hamilton 1964). Competiton is at the core of many theoretical and empirical studies of dispersal (Lambin et al. 2001), yet theory has shown early on that such ecological benefits are not a necessary requirement for dispersal to evolve as a strategy for avoiding kin-competition in stable habitats (Hamilton and May 1977). Rather, the evolution of dispersal could be viewed as an altruistic behavior, providing no direct ecological benefit to the dispersed individual, but alleviating competition with its kin (Hamilton and May 1977, Ronce 2007). Assuming that interactions between kin have the same direct fitness costs as interactions between non-kin, dispersal may result in siblings competing with nonsiblings at many sites instead of parents and offspring or siblings competing with themselves at a natal site (Hamilton and May 1977, Ronce et al. 2001). For some animals, the presence of kin within a patch may positively influence fitness, for instance through cooperative behavior. When dispersal is costly, dispersal may be selected against and provide the environment for the evolution of cooperative behavior which may be aided by kin selection (Hamilton 1964). Kin-biased

behaviors can increase inclusive fitness either directly or indirecty (Hamilton 1964). Kin selection has been widely accepted as a major factor shaping primate affiliative and cooperative behavior (Chapais 2001, Chapais and Belisle 2004, Silk 2002, 2007), especially in several ceropithecine primates (Gouzoules 1984, Gouzoules and Gouzoules 1987, Walters 1987, Silk 2002, Chapais 2006) but also some great apes (Watts 1994, Stewart and Harcourt 1987) and new world monkeys (Perry et al. 2008, Pope 1990, 2000). Female kin alliances have been primarily suggested to help gain access to food resources (Wrangham 1980, van Schaik 1989, Sterck et al. 1997) and research has suggested that this can have a positive influence on food intake (Koenig 2002). Female kin associations have been shown to improve female reproductive success, infant survival, longevity and, ultimately, fitness (Pope 1990, 2000, Silk 2002, Silk et al. 2003, 2009, 2010).

Even among the dispersing sex, same-sex matrilines or patrilines can develop over time if dispersal is a condition dependent tactic and there are benefits to cooperating with same-sexed kin for either ecological (Wrangham 1980, Sterck et al. 1997) or reproductive (e.g., Pope 1990, 2000) resources. However, living in a group does not necessarily mean living with kin, even for the pilopatric sex (Moore 1992, Lukas et al. 2005) and more importantly, having same-sexed kin in a social group does not necessarily translate into a bias towards nepotistic affiliative or cooperative behaviors (e.g., Seyfarth and Cheney 1984, Muroyama 1994, Henzi and Barrett 1999, Silk et al. 1999, Barrett et al. 2000, Mitani et al. 2002, Boesch et al. 2006, Langergraber et al. 2007). In fact, primate studies are providing more support for the prevelance and imporatance of non- or distantly related kin associations with individuals of similar age

or rank rather than with both maternal (Hashimoto et al. 1996, Mitani et al. 2002, Langergraber et al. 2007) or paternal (Langergraber et al. 2007) relatives. Thus, affiliation with non-kin is prevalent in many primates and may be more influential in some primate societies than kin-selection (Silk 2002, Chapais 2006, Langergraber et al. 2007). Reciprocity, regardless of kinship, may result in important benefits (Trivers 1971, Noë 2001) and other individual and social factors (e.g., group size, rank) should be considered as equally important variables for reproductive success and in both males and females.

Maternal effects on reproduction and development

In fact, mammalian life histories are influenced by genetic, demographic, ecological and social factors. Fitness is primarily dependent on an individual's genetic contribution into subsequent generations through offspring survival (Clutton-Brock 1988). In turn, offspring survival depends on their phenotype, which, in addition to genetic factors, can be affected by parental non-genetic factors such as maternal effects (overviews in Kirkpatrick and Lande 1989, Bernardo 1996, Mousseau and Fox 1998, Maestripieri and Mateo 2009). Maternal effects may influence offspring fitness in various ways, primarily through nutrition, behavioral or physiological mechanisms, or social effects such as group size or dominance rank (see summary in Maestripieri and Mateo 2009).

Female mammals invest substantially in both their pre- and postnatal contribution to offspring and maternal nutritional effects are suggested to have a particularly strong influence on infant development and survival in various mammals (Côté and Festa-

Bianchet 2001, Altmann and Alberts 2005, Gendreau et al. 2005, Vervaecke et al. 2005). Thus, access to resources is of prime importance in terms of female reproductive success in mammals (Wrangham 1980, van Schaik 1989), because levels of body fat affect ovulation, likelihood of conception, successful pregnancy and the ability to lactate (Koenig et al. 1997, McFarland 1997, Ellison 2003). In addition, it has been shown that a mother's nutritional condition influences the amount of milk yield, where females in better nutritional conditions produce a larger volume of milk compared to females in poorer condition (Landete-Castillejos et al. 2005, Hinde et al. 2009). Enhanced milk production has also been associated with accelerated infant development (Hinde 2007, Hinde et al. 2009).

Maternal nutritional effects among mammals have been dominated by studies of rodents and ungulates, while mammals with long life histories, such as nonhuman primates (Charnov and Berrigan 1993, Kappeler and Pereira 2003), have been underrepresented (see summary in Maestripieri and Mateo 2009). In nonhuman primates, offspring are born in an altricial state and tend to have slow growth rates compared to other mammals (Charnov and Berrigan 1993, Kappeler and Pereira 2003). This leads to considerable dependency of infants in the first years of life and a substantial burden on the mother through lactation (Altmann 1980, Lee 1987). Although nutritional requirements vary among mammals (overview in Tardif et al. 2001), this dependency is particularly crucial for survival through the first weeks of a primate infant's life since an older infant can supplement its mother's milk with foraging and ingesting foods independently. Consequently, nonhuman primates would make very suitable subjects for the study of maternal effects. However, both measures of maternal nutritional condition

and effects on infant growth and development are difficult to obtain for arboreal animals, including most primates, because the individuals are more difficult to observe.

In contrast, social maternal effects have been studied in some detail in terrestrial nonhuman primates such as baboons (Altamann 1980, Altmann and Alberts 2005). Among other aspects such as sex ratio adjustment or maternal effects on behavior (see overview in Maestripieri and Mateo 2009), it has been found that differences in dominance rank of mothers might be associated with substantial variation in offspring growth (e.g., Johnson 2003, Altmann and Alberts 2005). More generally, high rank of a mother may confer reproductive advantages in terms of shorter interbirth intervals or higher birth rates, likely indicating faster growth (Pusey et al. 1997, van Noordwijk and van Schaik 1999, Altmann and Alberts 2003). However, maternal rank effects on reproductive success have not always been found (see overview in Stockley and Bro-Jørgensen 2011). In theory, females may establish dominance relationships and gain better access to food if resources can be monopolized (Janson and van Schaik 1988, overview in Koenig 2002). Under these conditions, one expects females of high rank to gain more energy (Janson 1985, Vogel 2005) and therefore be in better nutritional condition (Koenig 2000). Thus, whether dominance rank indeed confers the predicted effects on offspring growth and reproductive success depends on an actual association of rank with energy gain and maternal nutritional condition, an association that has rarely been tested, especially in arboreal primates.

However, maternal condition may not be solely rank dependent and affected by direct competition over food, but may also depend on indirect (or scramble) competition (Janson and van Schaik 1988, van Schaik 1989, Giraldeau and Caraco 2000). As group

size (or density) increases, limiting food resources will be depleted faster, forcing individuals to increase foraging effort (Pyke 1984, Janson and van Schaik 1988, Chapman and Chapman 2000). As a result, individuals in large groups may be characterized by lower energy gain, which ultimately may lead to poorer maternal condition, slower growth, and reduced reproductive rates (Janson and van Schaik 1988, van Schaik 1989). While group size or density dependent effects on foraging effort or reproductive rate are well-known for nonhuman primates (van Noordwijk and van Schaik 1999, Altmann and Alberts 2005, Borries et al. 2008), the actual effects of maternal nutritional condition on infant development and growth are virtually unstudied (but see Altmann and Alberts 2005).

What is known about colobines?

For a number of reasons, Asian colobines provide a good model to investigate the influence of genetic and social structure on reproduction in a wild population. Colobines are best known for their specialized dietary adaptations for digesting leaves, and diets typically contain a relatively large proportion of leaves, but also fruits, seeds and occasionally flowers, animal byproducts and terrestrial vegetation or lichens (Koenig and Borries 2001, Fashing 2007, Kirkpatrick 2007, Sterck 2012). Colobines are generally described as arboreal primates with most species characterized by both male and female dispersal. They live in rather small groups, with polygynous one-male, multi-female groups and/ or promiscuous multi-male, multi-female units the norm and social relationships are generally described as rather tolerant. In terms of life history, colobines are generally assumed to be on the fast end of the “fast-slow continuum”, although

contradictory patterns in growth and development suggest that this categorization may be overly simplified (see below; Struhsaker 1975, Struhsaker and Leland 1987, Koenig and Borries 2001, Korstjens and Noe 2004, Arnold and Aureli 2007, Leigh et al. 2007, Kirkpatrick 2011, Sterck 2012).

Variability in dispersal patterns

To date, studies on dispersal in colobines have have focused on females due to the simple fact that female dispersal is so common in this subfamily. As a consequence, patterns and explanations for male dispersal strategies are typically underrepresented. Conflicting patterns of dispersal have been suggested for male colobines, with review papers generally describing males as the dispersing (Kirkpatrick 2011) or philopatric (Sterck 2012) sex. This disparity may be, in part, due to the extensive variability in colobines with some species characterized by male dispersal and female philopatry (Proboscis monkey, Boonratana 1999; guereza, Harris et al. 2009; Hanuman langur, Borries 2000, Koenig 2000, Koenig and Borries 2001; Nilgiri langurs, banded leaf-monkeys, purple-faced langurs, red leaf monkeys and guereza, Newton and Dunbar 1994), others by female dispersal and male philopatry (red colobus, Struhsaker and Leland 1979, Starin 1994), and still others by bisexual dispersal (olive colobus, Korstjens and Schippers 2003; Thomas's leaf monkey, Sterck et al. 2005; ursine colobus, Saj et al. 2007, Teichroeb and Sicotte 2009, Wikberg et al. 2012; golden snub-nosed monkeys, Zhao et al. 2008a, Yao et al. 2011, Yan 2012). However, few colobine studies have succeeded in combining observational and molecular data in describing dispersal patterns (but see *Colobus guereza*, Harris et al. 2009; *Colobus vellerosus*, Teichroeb et al. 2009,

Teichroeb and Sicotte 2011, Wikberg et al. 2012), particularly for Asian species (but see golden snub-nosed monkeys, Zhao et al. 2008a, Yan 2012).

Males should immigrate to increase mating opportunities, search for groups with a more favorable adult male/ adult female ratio, and to obtain higher rank. However, most of our knowledge on dispersal in colobine males comes from Hanuman langurs, which show a range of male options that are closely related to age, dominance, and seasonality in mating (Borries 2000). Reports of solitary males and all-male bands are common, and typically result from three circumstances: (1) aggressive eviction from natal groups (Hanuman langur, Treves and Chapman 1996; ursine colobus, Teichroeb and Sicotte 2011), voluntarily leaving previous groups (capped leaf monkeys, Stanford 1991b; ursine colobus, Teichroeb and Sicotte 2011), or being left by ther mothers (with male residents) following female secondary dispersal (Thomas's leaf monkey, Steenbeek et al. 2000). Solitary males may take over groups aggressively (Hanuman langur, Sugiyama 1965, Borries 2000; guereza, Struhsaker and Leland 1979; ursine colobus, Teichroeb and Sicotte 2011) or by attracting females and forming new groups (Marsh 1979b, Stanford 1991b, Sterck 1997, Sterck 2012). All-male bands may form due to predation risk and have also been observed to form coalitions to take over groups (Rajpurohit and Sommer 1993). While subordinate males may gain some mating opportunities or inclusive fitness benefits by remaining in a group with other males, all males should attempt to gain alpha positions, as rank and mating success is likely correlated (Borries 2000). Thus, decisions on whether to remain in or leave a group is likely dependent on age and if a young male in his prime doesn't achieve alpha position, he should emigrate. The dominant male should hold his positon for as long as he can and new males may attempt to force other

young males to leave (Rajpurohit and Sommer 1993, Borries 2000). Older males, however, may remain or disperse as long as they can gain some access to cycling females (Borries 2000).

Female transfer in colobines is common, particularly in Asian colobines (Yeager and Kool 2000, Sterck and van Hooff 2000), although the age and reproductive status of dispersing females may vary. While several colobine populations have only observed cases of natal dispersal by nulliparous females (red colobus, Struhsaker and Leland 1979), others have extensively documented both natal and secondarily dispersal (red colobus, Marsh 1979a,b; capped leaf monkeys, Stanford 1991b, Thomas's leaf monkey, Sterck et al. 2005; golden snub-nosed monkey, Zhao et al. 2008a; ursine colobus, Teichroeb et al. 2009). Natal dispersal is mainly suggested as a mechanism of inbreeding avoidance (Sterck and Korstjens 2000; olive colobus, Korstjens and Schippers 2003; golden snub-nosed monkey, Zhao et al. 2008a; but see ursine colobus, Teichroeb et al. 2009). Secondary dispersal seems to be a female strategy to avoid infanticide in some species. By transferring into smaller groups where infants might be less of a target (Hanuman langur, Treves and Chapman 1996; Thomas's leaf monkey, Steenbeek and van Schaik 2001), and leaving groups when extragroup males challenge resident males (Thomas's leaf monkey, Sterck 1997) or male group membership is unstable (ursine colobus, Teichroeb et al. 2009), females reduce the risk of infanticide. It has also been suggested that females join males who are better protectors against infanticide, and some evidence supports higher infant survival to infants born after dispersals than those born prior to dispersal (with the original males; Thomas's leaf monkey, Sterck et al. 2005). Females may also disperse to reduce competition over resources by transferring to groups

that are similar or smaller in size than their groups of origin (Thomas's leaf monkey, Sterck 1997; olive colobus, Korstjens and Schippers 2003; golden snub-nosed monkey, Zhao et al. 2008a; ursine colobus, Teichroeb et al. 2009).

Female dispersal can be voluntary (Thomas's leaf monkey, Sterck 1997) or forced when females are evicted from their group (king colobus, Korstjens et al. 2002; reviewed in Sterck and Korstjens 2000). Researchers rarely report solitary dispersing females ranging alone. While this may be an artifact of missed observations due to shy animals, it has also been suggested that female colobines disperse socially, joining adjacent social groups whose ranges overlap extensively with their own, strategically moving directly from one group into another (Isbell and van Vuren 1996). Females have also been observed to display parallel dispersal via same-sexed cohorts (e.g., red colobus, Starin 1991) or by following members of other species (e.g., olive colobus, Korstjens and Schippers 2003). And females may often join groups with familiar individuals and kin (Sterck et al. 2005, Teichroeb et al. 2009) or form new groups within their natal home range (Isbell and van Vuren 1996). Females may emigrate to follow and join (a) lone male(s) or transfer to a small, newly formed group (capped leaf monkey, Stanford 1991c; Thomas's leaf monkey, Steenbeek et al. 2000). In some species, however, dispersing females have been reported to disperse at large distances into entirely new home ranges (e.g., red colobus, Marsh 1979a, Starin 1994; olive colobus, Korstjens and Schippers 2003).

In some species, resident females may try to prevent immigrating females through directed aggression (ursine colobus, Teichroeb et al. 2009), while other species are typically more welcoming (Sterck et al. 2005, Sterck 2012). Female transfer between

existing groups may be a means of evaluating both females as well as male characteristics (Kirckpatrick 2011). It has been suggested that dispersing females with infants may be especially vulnerable to predation and infanticide by new males and typically disperse without dependent offspring (Sterck and Korstjens 2000). However, females may also transfer with dependent offspring (*T. johnii*, Poirier 1970; *P. siamensis*, Bennett 1983; *N. larvatus*, Bennett and Sebastian 1988), suggesting that infanticide risk in some species may be low.

Group composition and dynamics

Most colobines live in one-male, multiple-female groups (Moore 1999, Kirkpatrick 2011, Sterck 2012), where a single male is able to monopolize several females and sires most, if not all, offspring (Launhardt et al. 2001). Some colobines, however, consist of both one and multi-male groups (*Procolobus, Nasalis, Rhinopithecus,* some *Colobus, Trachypithecus* and *Semnopithecus*), which has been suggested to result from the maturation of natal males (Sterck and van Hooff 2000; Koenig and Borries 2012) or male immigration (Moore 1999, Borries and Koenig 2000). Some males are observed to join one-male groups with little aggression (Nilgiri langur, Poirier 1970; banded leaf monkey, Hohmann 1989, Megantara 1989). However, multi-male groups develop clear dominance hierarchies and alpha males have preferential mating access to females, but cannot always monopolize all females (red colobus, Struhsaker and Leland 1979, Struhsaker and Pope 1991, Starin 1994, Hanuman langurs: Borries and Koenig 2000, Launhardt et al. 2001; guereza, Harris and Monfort 2003). Group size in both one- and multi-male groups is surprisingly similar, although both vary and can include up to

15 adult females (Newton 1987, Sterck and van Hooff 2000, Kirkpatrick 2011). While some multi-male groups are stable over time, many are suggested to be transitional. Intra-group male contests can be sudden or gradual, but often result in one-male groups; where a resident male is either replaced by a maturing son or a new male (Kirkpatrick 2011). Natal multi-male groups often become age-graded (Thomas's leaf monkey, Steenbeek et al. 2000) and young adult males rarely replace their fathers as the sexually active male (Gurmaya 1986, Steenbeek et al. 2000) and often split, resulting in one-male groups (Nilgiri langur, Hohmann 1989). Most knowledge on stable multi-male groups comes from Hanuman langurs, where there are up to 5 adult males in the group, and males form dominance hierarchies that determine access to receptive females (Borries et al. 1999a). Immigrant males are often former residents of adjacent groups (Borries et al. 1999b) and while they may achieve all ranks, low rank may promote some males to transfer (Borries 2000). Thus, in addition to births and deaths, group changes in colobines appear to be driven by reproductive strategies, including both male competition and female choice. While males compete for access to females, females can choose to either remain or transfer (Kirkpatrick 2011). Intergroup relations appear to be mediated by both males and females and are not necessarily based solely on food defense (resource defense polygyny; Thomas's leaf monkey, Wich et al. 2002 a,b; guereza, Fashing 2001, Harris 2006). Intergroup encounters may facilitate female transfer (e.g., snub-nosed monkeys, Kirkpatrick 1998) and male-male aggression between groups or against new males serves to defend females (female defense polygyny), which has been observed in several colobine species (capped leaf monkey, Stanford 1991a; Thomas's leaf monkey,

Steenbeek et al. 2000, Wich et al. 2002b, Wich and Sterck 2007; king colobus, Korstjens et al. 2002)

Dominance interactions

Despite earlier suggestions (Wrangham 1980, Sterck et al. 1997), recent studies suggest that female colobines compete over food resources, have agonistic relationships, and display despotic dominance hierarchies (Hanuman langurs, Hrdy and Hrdy 1976, Borries et al. 1991, Borries 1993, Koenig 2000, Lu et al. 2008; Thomas's leaf monkey, Sterck and Steenbeek 1997; king colobus, Korstjens et al. 2002; Phayre's leaf monkey, Koenig et al. 2004a). However, unlike stable matrilineal hierarchies in cercopithecine females, dominance hierarchies are often individualistic (not based on kinship or coalition formation) and (inversely) age-graded, with frequent ranks changes (Hanuman, Borries et al. 1991; Phayre's leaf monkeys, Koenig et al. 2004a; guereza, Dunbar and Dunbar 1976; Hanuman langur, Borries 1993, Borries et al. 1991, Koenig 2000; king colobus, Korstjens et al. 2002; ursine colobus, Saj et al. 2007). There is also evidence linking dominance rank to access to food and female fitness. High-ranking female Hanuman langurs are in better body condition (Koenig 2000), ingest more food (Borries 1993), conceive earlier (Koenig et al. 1997), and more often (Borries et al. 1991) compared to low-ranking females. Observations of Thomas's leaf monkeys, on the other hand, have failed to show any influence of female dominance rank on time spent feeding, feeding intake, or reproductive success (Sterck 1995, Sterck et al. 1997). Thus, further studies exploring the impact of female dominance relationships on nutritional condition and reproduction are needed.

Life history

Colobine life history has generally been reported as "fast", with females giving birth at a younger age, having more offspring over the lifespan, and living shorter lives compared to frugivorous primates of similar body size (Leigh 1994, Wich et al. 2007). However, recent studies have called this idea into question suggesting that colobines might have aspects of life history that are slower (e.g., gestation) compared to cercopithecines (Borries et al. 2011).

Colobine life histories are also influenced by nutritional factors. For instance, provisioning or food abundance are known accelerate age at first reproduction (reviewed in Sterck 2012), increase the probability of conception (e.g., *Rhinopithecus bieti*, Xiang and Sayers 2009; *Semnopithecus entellus*, Koenig et al. 1997; *Trachypithecus leucocephalus*, Jin et al. 2009; *T. phayrei*, Borries and Koenig 2005, reviewed in Brockman and van Schaik 2005), reduce the length of interbirth intervals (e.g., Borries et al. 2001; reviewed in Sterck 2012), and accelerate weaning (white-headed black leaf monkey, Zhao et al. 2008b; silver leaf monkey, Shelmidine et al. 2009). In Hanuman langurs, the pace of life history, as measured by the frequency of births (IBI), is also influenced by social rank, an unsurprising result, given the association between rank and food intake / body condition.

Natal coloration

An interesting aspect of colobines that has received widespread attention is the fact that colobine infants are typically born with natal coloration that changes over the

first months of life (Treves 1997). Natal coats are found in all but one species of colobine (*N. narvatus*, Newton and Dunbar 1994). Most are conspicuous in color and mainly suggested to have evolved to attract female caretakers (infant handling or alloparenting, Hrdy 1976, but see Newton and Dunbar 1994, Treves 1997). Non-maternal caretakers (alloparents) are virtually ubiquitous in colobine monkeys, but there are some exceptions (e.g., red colobus, olive colobus; McKenna 1979; Newton and Dunbar 1994). In fact, red and olive colobus are believed to have darker natal coats due the lack of infant handling. However, the darker coat in Hanuman infants is more likely attributed to camouflage due to the high risks of predation and infanticide (Newton and Dunbar 1994). Infant handling is typical for females, and males may be more tolerant of infants but will alloparent on occasion and more often protect infants (Whitten 1987, Borries et al. 1999b; Kirkpatrick 2011, Sterck 2012). Nonetheless, in addition to improving maternal reproduction, allomothering may have important fitness benefits and costs for mothers, allomothers, and infants (Stanford 1992, Mitani and Watts 1997).

However, less is known about the direct relationship between maternal nutrition, energy transfer via lactation, and early infant development. It remains unclear whether speed of natal color change is a direct consequence of differences in the amount and quality of milk and whether this correlates with body mass of infants. However, several studies strongly support an effect of maternal body mass or fatness on growth rates of infants in both captive as well as wild populations of primates and other mammals (Johnson 2003, Altmann and Alberts 2005, Vervaecke et al. 2005, Hinde et al. 2009, Landete-Castillejos et al. 2010). Thus, it is likely that there are developmental implications for skin and pelage variables (Sumner and Mollon 2003, Bradley and

Mundy 2008). While some previous studies indicated that pelage chromaticities do not change much with the environment or the diet (captive versus wild; Sumner and Mollon 2003), other studies point to the importance of both genetic and environmental influences for the development of coat color (Caro 2005, Bradley and Mundy 2008). While the transition from natal to adult pelage is likely genetically pre-determined, the speed of melanin-based hair color change could also reflect nutritional condition or hormone levels. If and how diet and nutrition directly influence melanin pigmentation in primates is still largely unknown (Bradley and Mundy 2008). In general, it seems clear that access to adequate dietary nutrients can influence pigmentation in birds (Baker and Parker 1979) and mammals (Mundy et al. 1998, West and Packer 2002), which likely indicates that gene expression is sensitive to nutritional status (Roulin 2009). Thus, any variation in natal color change resulting from different maternal nutritional conditions could indicate an environmental influence in the transition from natal to adult coloration.

Phayre's leaf monkeys

Phayre's leaf monkeys (*Trachypithecus phayrei*) are an Asian colobine that occur in eastern Bangladesh, southwestern China, northeastern India, Lao PDR, Myanmar, Thailand (north of the peninsular zone) and northern Vietnam (Groves 2001). The species prefers primary and secondary evergreen and semi-evergreen forest, mixed moist deciduous forest, but is also found in bamboo-dominated areas, light woodlands, near tea plantations and in limestone forest (Nadler et al. 2005, 2007). The species is listed under the IUCN Red List as endangered ((EN) Criteria: A2cd; CITES Appendix II, IUCN 2013) as it has undergone a decline of more than 50% over the last three generations due to a combination of habitat loss and hunting (Bleisch et al. 2008). *T. phayrei* is recognized by IUCN to include three subspecies (*T. p. phayrei, T. p. crepuscula* and *T. p. shanicus*).

The study subspecies, *T. p. crepusculus*, occurs in southwestern China (central, southern and southwestern Yunnan, with the Salween River as its western boundary), Lao PDR, Myanmar (north of the peninsular zone south of the range of *T. p. phayrei* and west to the coast of the Bay of Bengal), northern Vietnam, and Thailand (north of the peninsular zone and range of *T. obscurus*) (Groves 2001). While originally described as a distinct species (*Pithecus crepuscula*, Eliot 1909), the taxon has been traditionally recognized as a subspecies of *T. phayrei* because of similar coloration (Napier and Napier 1967, Corbet and Hill 1992, Groves 2001) and recent molecular data suggest that it is a distinct species resulting in introgression or ancestral hybridization between two species groups (*T. obscurus* and *T. francoisi* groups; Geissman et al. 2004, Roos et al. 2007). Roos and colleagues found a distinct clustering of the Indochinese grey langur (*T. crepusculus*) with a distribution in northern Vietnam, southernmost China, Laos and central and northwest Thailand (Roos et al. 2007). While systematic classification for the population Phu Khieo Wildlife Sanctuary is underway (unpublished), the taxon is phenotypically distinguished by its light coat coloration, light eyerings, and depigmented skin over its lips (Groves 2001).

Overall, the species is reported to have a serious ongoing global decline due to hunting (for traditional medicine and bushmeat) and habitat disturbance, although the wild populations in Thailand are some of the best protected. Only two field studies have been conducted on Phayre’s leaf monkeys, including one in Tripura, India (*T. p. phayrei*,

Acknowledgements

(*not yet finished*)

Chapter 1

Introduction and Summary of Chapters

Dispersal Theory

Dispersal patterns, social structure, and individual reproductive success influence genetic variation within and among social groups across space and time (Altmann et al. 1996, Clobert et al. 2001, Gandon and Michalakis 2001, Vigilant et al. 2001, Di Fiore 2009, Lukas and Clutton-Brock 2011). Dispersal affects inbreeding (Roze and Rousset 2003, Gandon 1999, Pusey and Wolf 1996), social relationships (Le Galliard et al. 2005, Silk 2002), an individual's life history (e.g., Pen 2000), and the evolution of species (see review in Barton 2001).

A central goal of dispersal theory, and particularly sex-biases in dispersal, includes understanding both the ultimate (evolutionary) and proximate (immediate mechanistic or social factors) causes of dispersal (Hamilton and May 1977, Pusey and Wolf 1996, Gandon and Michalakis 2001, Lawson Handley and Perrin 2007, Long et al. 2008). Ultimate causes of dispersal include: (1) inbreeding avoidance (Packer 1979, Dobson 1982, Shields 1982, Waser et al. 1986, Pusey 1987, Clutton-Brock 1989, Pusey and Wolf 1996, Gandon 1999, Lukas and Clutton-Brock 2011, Clutton-Brock and Lukas 2012), (2) reducing mate competition (Dobson 1982, Hamilton 1967, Moore and Ali 1984), and (3) reducing competition for resources (Murray 1967, Clarke 1978, Greenwood 1980, 1983, Pusey and Packer 1987, Shields 1987, Bowler and Benton 2005, Ronce et al. 2001). On the other hand, the importance of social relationships (e.g., Silk et al. 2003), group size and with it increased aggression and competition (e.g., Watts 1994,

Pope 2000, Stokes et al. 2003), and intrasexual competition (density dependent increases in aggression; Moore and Ali 1984, Pope 2000, Clobert et al. 2004, Bonenfant et al. 2009) have been described in proximate dispersal decisions. In this regard, genetic relationships are considered fundamental in understanding dispersal decisions (Hamilton 1964, Greenwood 1980, Pusey 1987; Clutton-Brock 1989, Pusey and Wolf 1996, Sterck et al. 1997, Lawson Handley and Perrin 2007). Studies have shown strong support for the effect of kin interactions on dispersal decisions including contexts favoring an individual to stay in the presence of kin potentially increasing inclusive fitness through cooperation (e.g., Hamilton 1964, Wrangham 1980, Sterck et al. 1997) and contexts favoring an individual to leave due to competition (e.g., Hamilton and May 1977, Gandon 1999), particularly in relation to ecological and reproductive constraints (Wrangham 1980, Sterck et al. 1997, Bowler and Benton 2005, Ronce et al. 2001). The latter may lead to avoidance of kin in an attempt to avoid kin competition (Hamilton and May 1977, Gandon 1999, Ronce 2007).

For many taxa, especially birds and mammals, groups exhibit sex-biased dispersal patterns where males and females differ in their age at dispersal, dispersal distance, or other characteristics (for review see Lawson Handley and Perrin 2007). Complete bias in dispersal, where one sex remains exclusively philopatric, is rare in mammals but generally more common in birds and to some degree in primates (Pusey and Packer 1987, Greenwood 1980, Johnson and Gaines 1990, Lawson Handley and Perrin 2007, Lukas and Clutton-Brock 2011). Inbreeding avoidance and the reduction of competition over resources have been suggested to increase the fitness of same-sexed conspecifics often resulting in sex-biases in dispersal (Greenwood 1980, Gandon 1999, Matthysen 2005,

Lawson Handley and Perrin 2007, Gros et al. 2008). For many social mammals and birds, males typically emigrate from their natal group and females remain philopatric, or in their natal group throughout a lifetime (Greenwood 1980, Pusey and Packer 1987). This trend has been widely found in studies of most cercopithecine primates (Wrangham 1980, Melnick and Pearl 1987, Pusey and Packer 1987, Clutton-Brock 2009). However, in several strepsirrhine, platyrrhine, colobine, and hominoid primates, females are the predominant dispersers or both sexes disperse but at varying distances or ages (Moore 1984, Pusey and Packer 1987, Pope 1992, Strier 1994, Nishimura 2003, Stokes et al. 2003, Di Fiore 2003, Bradley et al. 2004, Bradley et al. 2007, Douadi et al. 2007, Huck et al. 2007, Lawson-Handley and Perrin 2007, Morelli et al. 2009, Di Fiore 2009, Di Fiore et al. 2009, Clutton-Brock and Lucas 2012, Yan 2012, Inoue et al. 2013)

Research on female dispersal species has been important in challenging primate socio-ecological models (Wrangham 1980, van Schaik 1989, Sterck et al. 1997) and female dispersal species appear to display more social complexity than previously thought (Moore 1999, but see Clutton-Brock and Lukas 2012); to a point that predictions about dispersal in socio-ecological models have been questioned (Koenig and Borries 2009, Clutton-Brock and Janson 2012). Similar to other social animals, female dispersal in nonhuman primates has commonly been linked to inbreeding avoidance (Moore 1984, Watts 1990, Clutton-Brock 1989, Sterck 1997, Starin 2001, Bradley et al. 2007, Lukas and Clutton-Brock 2011, Clutton-Brock and Lukas 2012), but infanticide avoidance (Crockett and Janson 2000, Stokes et al. 2003, Watts 1990, Sterck 1997, Lukas and Clutton-Brock 2011) and the reduction in scramble competition (e.g., Jones 1980, Wrangham 1980, Glander 1992, Sterck 1997, 1998, Crockett and Janson 2000) has also

been suggested to shape female dispersal decisions. In addition, context dependent strategies often vary for natal versus secondary dispersers (Pusey and Packer 1987, Pope 2000, Starin 2001, Stokes et al. 2003).

Similar to other social animals, genetic relatedness is considered a principle characteristic driving the structure of social groups and suggested to have direct influences on ecological and social contexts in gregarious primates (Wrangham 1980, Isbell 1991, Moore 1992, van Schaik 1989, Sterck et al. 1997). Recent studies have shown how non-random dispersal may result in groups with same-sexed kin (Starin 1994, Watts 1994, Pope 2000, Lukas et al. 2005, Bradley et al. 2007) via cohort dispersal (Starin 1994, Watts 1994, Bradley et al. 2007) or dispersing into groups consisting of related natal females (Starin 1994). In addition, despite initial dispersal, female kin groups can develop over time (Pope 2000) or additional social or anthropogenic factors that may lead to groups disbanding (Stokes et al. 2003, Di Fiore 2009) could result in groups containing female relatives despite female dispersal. This opportunity to overlap with kin despite dispersal could provide the potential for kin-biased behaviors (Chapais 2001, Bradley et al. 2007). Molecular studies have also shown how it is possible that gene flow within a population can still be mediated through the more philopatric sex (Schubert et al. 2011) or dispersal distances may be underrepresented by sampling methodology (Inoue et al. 2013). Patterns of within group genetic relatedness may also be influenced if there is a high reproductive skew among males within social groups, which results in cohorts of similarly aged individuals being more closely related to one another through common paternity than are animals of different ages (e.g., Pope 1990, Widdig et al. 2001, 2002). Similarly, extra-group mating by either males or females can act to

reduce the extent of genetic differentiation between groups (Vigilant et al. 2001, Di Fiore 2009).

However, long-term demographic, social and genetic data on group-living female dispersal species are comparatively rare. Long-term databases for chimpanzees (Pusey 1979, Pusey et al. 1997, Vigilant et al. 2001, Langergraber et al. 2007), bonobos (Kano 1992), gorillas (Harcourt 1978, Stokes et al. 2003, Bradley et al. 2007), hamadryas baboons (Sigg et al. 1982), African colobines (Starin 1994, Korstjens and Schippers 2003, Teichroeb et al. 2009, Wikberg et al. 2012, Minhós et al. 2013), Asian colobines (Poirier 1969, 1970, Rudran 1973, Newton 1987, Kool 1989, Stanford 1991, Sterck 1997, Borries et al. 2004, Yan 2012), Atelids (Symington 1987, Strier 1990, Strier 1994, Crocket and Pope 1993, Ellsworth 2000, Nishimura 2003, Di Fiore and Fleischer 2005, Di Fiore and Campbell 2007, Di Fiore et al. 2009), squirrel monkeys (Mitchell et al. 1991, Blair and Melnick 2012), and lemurs (Morelli et al. 2009) have received more attention. Relatively few studies, however, actually use molecular data to investigate links between female dispersal patterns, kinship, and social behavior (i.e., Hohmann et al. 1999, Pope 2000, Mitani et al. 2002, Stokes et al. 2003, Di Fiore and Fleischer 2005, Langergraber et al. 2007, Morelli et al. 2009, Di Fiore 2009, Di Fiore et al. 2009, Yan 2012). Even fewer explore these variables in relation to either male (Pope 1990, Vigilant et al. 2001, Bradley et al. 2005, Boesch et al. 2006, Langergraber et al. 2007, Inoue et al. 2008, Nsubuga et al. 2008, Inoue et al. 2013) or female (i.e., Pusey et al. 1997, Pope 2000, Stokes et al. 2003) reproductive success.

Kin recognition

A basic assumption of kin selection theory is that individuals have the ability to decipher relatives either through kin recognition or discrimination, which is still debated in the literature (e.g., Blaustein et al. 1991, Chapais et al. 1997, Rendall 2004, Holmes and Mateo 2007). Proper kin recognition allows altruistic acts to be directed to the right recipient and avoid inbreeding. However, while primates are believed to exhibit finely developed kin recognition abilities (Silk 2002), using locational cues for kin recognition is not believed to be effective for gregarious species (Hamilton 1987), such as primates.

In fact, studies of young monkeys found no discrimination among kin and nonkin during interactions when familiarity was held constant (MacKenzie et al. 1985, Sackett and Frederickson 1987, Welker et al. 1987, Erhart et al. 1997, Martin 1997, Widdig et al. 2001). Most research also suggests that since primates rely on familiarity, individuals cannot recognize paternal kin since larger social groups often contain several potential sires and discriminating kin from non-kin would rely on the ability to recognize familial alleles or phenotypic matching (Gouzoules and Gouzoules 1987, Chapais 1995, Mitani et al. 2000). Preliminary studies suggest baboons may decipher individuals that exhibit familial cues (Alberts 1999, Smith 2000) and some evidence shows situation dependent recognition of paternal-kin (Widdig et al. 2001, 2002). However, a criticism of the latter study is that this bias could also result from a preference for age-related cohorts that happened to be sired by a high-ranking male rather than inert recognition (Altmann 1979, Smith et al. 2003, Chapais and Berman 2004, Rendall 2004). Nontheless, there is still little support for the preference of maternal siblings, which should be preferred similarly to paternal kin given equal levels of relatedness (Chapais and Berman 2004). To date, the most support for kin recognition among primates is through the mechanism of familiarity

with individuals during early development (Rendall 2004). Thus, primate studies have shown the most support for familiarity, independent of genetic relatedness, to play an important role in shaping social behaviors in primates

Competition and cooperation among kin and non-kin

Kinship can be a proximate mechanism triggering dispersal to avoid inbreeding or kin competition (Pusey and Wolf 1996, Ronce et al. 2001) or as a means to formulate affiliative and cooperative relationships with relatives. According to Hamilton's rule, selection will depend on the balance between the inclusive fitness benefits of the trait and the direct fitness costs to the individual (Hamilton 1964). Competiton is at the core of many theoretical and empirical studies of dispersal (Lambin et al. 2001), yet theory has shown early on that such ecological benefits are not a necessary requirement for dispersal to evolve as a strategy for avoiding kin-competition in stable habitats (Hamilton and May 1977). Rather, the evolution of dispersal could be viewed as an altruistic behavior, providing no direct ecological benefit to the dispersed individual, but alleviating competition with its kin (Hamilton and May 1977, Ronce 2007). Assuming that interactions between kin have the same direct fitness costs as interactions between non-kin, dispersal may result in siblings competing with nonsiblings at many sites instead of parents and offspring or siblings competing with themselves at a natal site (Hamilton and May 1977, Ronce et al. 2001). For some animals, the presence of kin within a patch may positively influence fitness, for instance through cooperative behavior. When dispersal is costly, dispersal may be selected against and provide the environment for the evolution of cooperative behavior which may be aided by kin selection (Hamilton 1964). Kin-biased

behaviors can increase inclusive fitness either directly or indirecty (Hamilton 1964). Kin selection has been widely accepted as a major factor shaping primate affiliative and cooperative behavior (Chapais 2001, Chapais and Belisle 2004, Silk 2002, 2007), especially in several ceropithecine primates (Gouzoules 1984, Gouzoules and Gouzoules 1987, Walters 1987, Silk 2002, Chapais 2006) but also some great apes (Watts 1994, Stewart and Harcourt 1987) and new world monkeys (Perry et al. 2008, Pope 1990, 2000). Female kin alliances have been primarily suggested to help gain access to food resources (Wrangham 1980, van Schaik 1989, Sterck et al. 1997) and research has suggested that this can have a positive influence on food intake (Koenig 2002). Female kin associations have been shown to improve female reproductive success, infant survival, longevity and, ultimately, fitness (Pope 1990, 2000, Silk 2002, Silk et al. 2003, 2009, 2010).

Even among the dispersing sex, same-sex matrilines or patrilines can develop over time if dispersal is a condition dependent tactic and there are benefits to cooperating with same-sexed kin for either ecological (Wrangham 1980, Sterck et al. 1997) or reproductive (e.g., Pope 1990, 2000) resources. However, living in a group does not necessarily mean living with kin, even for the pilopatric sex (Moore 1992, Lukas et al. 2005) and more importantly, having same-sexed kin in a social group does not necessarily translate into a bias towards nepotistic affiliative or cooperative behaviors (e.g., Seyfarth and Cheney 1984, Muroyama 1994, Henzi and Barrett 1999, Silk et al. 1999, Barrett et al. 2000, Mitani et al. 2002, Boesch et al. 2006, Langergraber et al. 2007). In fact, primate studies are providing more support for the prevelance and imporatance of non- or distantly related kin associations with individuals of similar age

or rank rather than with both maternal (Hashimoto et al. 1996, Mitani et al. 2002, Langergraber et al. 2007) or paternal (Langergraber et al. 2007) relatives. Thus, affiliation with non-kin is prevalent in many primates and may be more influential in some primate societies than kin-selection (Silk 2002, Chapais 2006, Langergraber et al. 2007). Reciprocity, regardless of kinship, may result in important benefits (Trivers 1971, Noë 2001) and other individual and social factors (e.g., group size, rank) should be considered as equally important variables for reproductive success and in both males and females.

Maternal effects on reproduction and development

In fact, mammalian life histories are influenced by genetic, demographic, ecological and social factors. Fitness is primarily dependent on an individual's genetic contribution into subsequent generations through offspring survival (Clutton-Brock 1988). In turn, offspring survival depends on their phenotype, which, in addition to genetic factors, can be affected by parental non-genetic factors such as maternal effects (overviews in Kirkpatrick and Lande 1989, Bernardo 1996, Mousseau and Fox 1998, Maestripieri and Mateo 2009). Maternal effects may influence offspring fitness in various ways, primarily through nutrition, behavioral or physiological mechanisms, or social effects such as group size or dominance rank (see summary in Maestripieri and Mateo 2009).

Female mammals invest substantially in both their pre- and postnatal contribution to offspring and maternal nutritional effects are suggested to have a particularly strong influence on infant development and survival in various mammals (Côté and Festa-

Bianchet 2001, Altmann and Alberts 2005, Gendreau et al. 2005, Vervaecke et al. 2005). Thus, access to resources is of prime importance in terms of female reproductive success in mammals (Wrangham 1980, van Schaik 1989), because levels of body fat affect ovulation, likelihood of conception, successful pregnancy and the ability to lactate (Koenig et al. 1997, McFarland 1997, Ellison 2003). In addition, it has been shown that a mother's nutritional condition influences the amount of milk yield, where females in better nutritional conditions produce a larger volume of milk compared to females in poorer condition (Landete-Castillejos et al. 2005, Hinde et al. 2009). Enhanced milk production has also been associated with accelerated infant development (Hinde 2007, Hinde et al. 2009).

Maternal nutritional effects among mammals have been dominated by studies of rodents and ungulates, while mammals with long life histories, such as nonhuman primates (Charnov and Berrigan 1993, Kappeler and Pereira 2003), have been underrepresented (see summary in Maestripieri and Mateo 2009). In nonhuman primates, offspring are born in an altricial state and tend to have slow growth rates compared to other mammals (Charnov and Berrigan 1993, Kappeler and Pereira 2003). This leads to considerable dependency of infants in the first years of life and a substantial burden on the mother through lactation (Altmann 1980, Lee 1987). Although nutritional requirements vary among mammals (overview in Tardif et al. 2001), this dependency is particularly crucial for survival through the first weeks of a primate infant's life since an older infant can supplement its mother's milk with foraging and ingesting foods independently. Consequently, nonhuman primates would make very suitable subjects for the study of maternal effects. However, both measures of maternal nutritional condition

and effects on infant growth and development are difficult to obtain for arboreal animals, including most primates, because the individuals are more difficult to observe.

In contrast, social maternal effects have been studied in some detail in terrestrial nonhuman primates such as baboons (Altamann 1980, Altmann and Alberts 2005). Among other aspects such as sex ratio adjustment or maternal effects on behavior (see overview in Maestripieri and Mateo 2009), it has been found that differences in dominance rank of mothers might be associated with substantial variation in offspring growth (e.g., Johnson 2003, Altmann and Alberts 2005). More generally, high rank of a mother may confer reproductive advantages in terms of shorter interbirth intervals or higher birth rates, likely indicating faster growth (Pusey et al. 1997, van Noordwijk and van Schaik 1999, Altmann and Alberts 2003). However, maternal rank effects on reproductive success have not always been found (see overview in Stockley and Bro-Jørgensen 2011). In theory, females may establish dominance relationships and gain better access to food if resources can be monopolized (Janson and van Schaik 1988, overview in Koenig 2002). Under these conditions, one expects females of high rank to gain more energy (Janson 1985, Vogel 2005) and therefore be in better nutritional condition (Koenig 2000). Thus, whether dominance rank indeed confers the predicted effects on offspring growth and reproductive success depends on an actual association of rank with energy gain and maternal nutritional condition, an association that has rarely been tested, especially in arboreal primates.

However, maternal condition may not be solely rank dependent and affected by direct competition over food, but may also depend on indirect (or scramble) competition (Janson and van Schaik 1988, van Schaik 1989, Giraldeau and Caraco 2000). As group

size (or density) increases, limiting food resources will be depleted faster, forcing individuals to increase foraging effort (Pyke 1984, Janson and van Schaik 1988, Chapman and Chapman 2000). As a result, individuals in large groups may be characterized by lower energy gain, which ultimately may lead to poorer maternal condition, slower growth, and reduced reproductive rates (Janson and van Schaik 1988, van Schaik 1989). While group size or density dependent effects on foraging effort or reproductive rate are well-known for nonhuman primates (van Noordwijk and van Schaik 1999, Altmann and Alberts 2005, Borries et al. 2008), the actual effects of maternal nutritional condition on infant development and growth are virtually unstudied (but see Altmann and Alberts 2005).

What is known about colobines?

For a number of reasons, Asian colobines provide a good model to investigate the influence of genetic and social structure on reproduction in a wild population. Colobines are best known for their specialized dietary adaptations for digesting leaves, and diets typically contain a relatively large proportion of leaves, but also fruits, seeds and occasionally flowers, animal byproducts and terrestrial vegetation or lichens (Koenig and Borries 2001, Fashing 2007, Kirkpatrick 2007, Sterck 2012). Colobines are generally described as arboreal primates with most species characterized by both male and female dispersal. They live in rather small groups, with polygynous one-male, multi-female groups and/ or promiscuous multi-male, multi-female units the norm and social relationships are generally described as rather tolerant. In terms of life history, colobines are generally assumed to be on the fast end of the “fast-slow continuum”, although

contradictory patterns in growth and development suggest that this categorization may be overly simplified (see below; Struhsaker 1975, Struhsaker and Leland 1987, Koenig and Borries 2001, Korstjens and Noe 2004, Arnold and Aureli 2007, Leigh et al. 2007, Kirkpatrick 2011, Sterck 2012).

Variability in dispersal patterns

To date, studies on dispersal in colobines have have focused on females due to the simple fact that female dispersal is so common in this subfamily. As a consequence, patterns and explanations for male dispersal strategies are typically underrepresented. Conflicting patterns of dispersal have been suggested for male colobines, with review papers generally describing males as the dispersing (Kirkpatrick 2011) or philopatric (Sterck 2012) sex. This disparity may be, in part, due to the extensive variability in colobines with some species characterized by male dispersal and female philopatry (Proboscis monkey, Boonratana 1999; guereza, Harris et al. 2009; Hanuman langur, Borries 2000, Koenig 2000, Koenig and Borries 2001; Nilgiri langurs, banded leaf-monkeys, purple-faced langurs, red leaf monkeys and guereza, Newton and Dunbar 1994), others by female dispersal and male philopatry (red colobus, Struhsaker and Leland 1979, Starin 1994), and still others by bisexual dispersal (olive colobus, Korstjens and Schippers 2003; Thomas's leaf monkey, Sterck et al. 2005; ursine colobus, Saj et al. 2007, Teichroeb and Sicotte 2009, Wikberg et al. 2012; golden snub-nosed monkeys, Zhao et al. 2008a, Yao et al. 2011, Yan 2012). However, few colobine studies have succeeded in combining observational and molecular data in describing dispersal patterns (but see *Colobus guereza*, Harris et al. 2009; *Colobus vellerosus*, Teichroeb et al. 2009,

Teichroeb and Sicotte 2011, Wikberg et al. 2012), particularly for Asian species (but see golden snub-nosed monkeys, Zhao et al. 2008a, Yan 2012).

Males should immigrate to increase mating opportunities, search for groups with a more favorable adult male/ adult female ratio, and to obtain higher rank. However, most of our knowledge on dispersal in colobine males comes from Hanuman langurs, which show a range of male options that are closely related to age, dominance, and seasonality in mating (Borries 2000). Reports of solitary males and all-male bands are common, and typically result from three circumstances: (1) aggressive eviction from natal groups (Hanuman langur, Treves and Chapman 1996; ursine colobus, Teichroeb and Sicotte 2011), voluntarily leaving previous groups (capped leaf monkeys, Stanford 1991b; ursine colobus, Teichroeb and Sicotte 2011), or being left by ther mothers (with male residents) following female secondary dispersal (Thomas's leaf monkey, Steenbeek et al. 2000). Solitary males may take over groups aggressively (Hanuman langur, Sugiyama 1965, Borries 2000; guereza, Struhsaker and Leland 1979; ursine colobus, Teichroeb and Sicotte 2011) or by attracting females and forming new groups (Marsh 1979b, Stanford 1991b, Sterck 1997, Sterck 2012). All-male bands may form due to predation risk and have also been observed to form coalitions to take over groups (Rajpurohit and Sommer 1993). While subordinate males may gain some mating opportunities or inclusive fitness benefits by remaining in a group with other males, all males should attempt to gain alpha positions, as rank and mating success is likely correlated (Borries 2000). Thus, decisions on whether to remain in or leave a group is likely dependent on age and if a young male in his prime doesn't achieve alpha position, he should emigrate. The dominant male should hold his positon for as long as he can and new males may attempt to force other

young males to leave (Rajpurohit and Sommer 1993, Borries 2000). Older males, however, may remain or disperse as long as they can gain some access to cycling females (Borries 2000).

Female transfer in colobines is common, particularly in Asian colobines (Yeager and Kool 2000, Sterck and van Hooff 2000), although the age and reproductive status of dispersing females may vary. While several colobine populations have only observed cases of natal dispersal by nulliparous females (red colobus, Struhsaker and Leland 1979), others have extensively documented both natal and secondarily dispersal (red colobus, Marsh 1979a,b; capped leaf monkeys, Stanford 1991b, Thomas's leaf monkey, Sterck et al. 2005; golden snub-nosed monkey, Zhao et al. 2008a; ursine colobus, Teichroeb et al. 2009). Natal dispersal is mainly suggested as a mechanism of inbreeding avoidance (Sterck and Korstjens 2000; olive colobus, Korstjens and Schippers 2003; golden snub-nosed monkey, Zhao et al. 2008a; but see ursine colobus, Teichroeb et al. 2009). Secondary dispersal seems to be a female strategy to avoid infanticide in some species. By transferring into smaller groups where infants might be less of a target (Hanuman langur, Treves and Chapman 1996; Thomas's leaf monkey, Steenbeek and van Schaik 2001), and leaving groups when extragroup males challenge resident males (Thomas's leaf monkey, Sterck 1997) or male group membership is unstable (ursine colobus, Teichroeb et al. 2009), females reduce the risk of infanticide. It has also been suggested that females join males who are better protectors against infanticide, and some evidence supports higher infant survival to infants born after dispersals than those born prior to dispersal (with the original males; Thomas's leaf monkey, Sterck et al. 2005). Females may also disperse to reduce competition over resources by transferring to groups

that are similar or smaller in size than their groups of origin (Thomas's leaf monkey, Sterck 1997; olive colobus, Korstjens and Schippers 2003; golden snub-nosed monkey, Zhao et al. 2008a; ursine colobus, Teichroeb et al. 2009).

Female dispersal can be voluntary (Thomas's leaf monkey, Sterck 1997) or forced when females are evicted from their group (king colobus, Korstjens et al. 2002; reviewed in Sterck and Korstjens 2000). Researchers rarely report solitary dispersing females ranging alone. While this may be an artifact of missed observations due to shy animals, it has also been suggested that female colobines disperse socially, joining adjacent social groups whose ranges overlap extensively with their own, strategically moving directly from one group into another (Isbell and van Vuren 1996). Females have also been observed to display parallel dispersal via same-sexed cohorts (e.g., red colobus, Starin 1991) or by following members of other species (e.g., olive colobus, Korstjens and Schippers 2003). And females may often join groups with familiar individuals and kin (Sterck et al. 2005, Teichroeb et al. 2009) or form new groups within their natal home range (Isbell and van Vuren 1996). Females may emigrate to follow and join (a) lone male(s) or transfer to a small, newly formed group (capped leaf monkey, Stanford 1991c; Thomas's leaf monkey, Steenbeek et al. 2000). In some species, however, dispersing females have been reported to disperse at large distances into entirely new home ranges (e.g., red colobus, Marsh 1979a, Starin 1994; olive colobus, Korstjens and Schippers 2003).

In some species, resident females may try to prevent immigrating females through directed aggression (ursine colobus, Teichroeb et al. 2009), while other species are typically more welcoming (Sterck et al. 2005, Sterck 2012). Female transfer between

existing groups may be a means of evaluating both females as well as male characteristics (Kirckpatrick 2011). It has been suggested that dispersing females with infants may be especially vulnerable to predation and infanticide by new males and typically disperse without dependent offspring (Sterck and Korstjens 2000). However, females may also transfer with dependent offspring (*T. johnii*, Poirier 1970; *P. siamensis*, Bennett 1983; *N. larvatus*, Bennett and Sebastian 1988), suggesting that infanticide risk in some species may be low.

Group composition and dynamics

Most colobines live in one-male, multiple-female groups (Moore 1999, Kirkpatrick 2011, Sterck 2012), where a single male is able to monopolize several females and sires most, if not all, offspring (Launhardt et al. 2001). Some colobines, however, consist of both one and multi-male groups (*Procolobus, Nasalis, Rhinopithecus,* some *Colobus, Trachypithecus* and *Semnopithecus*), which has been suggested to result from the maturation of natal males (Sterck and van Hooff 2000; Koenig and Borries 2012) or male immigration (Moore 1999, Borries and Koenig 2000). Some males are observed to join one-male groups with little aggression (Nilgiri langur, Poirier 1970; banded leaf monkey, Hohmann 1989, Megantara 1989). However, multi-male groups develop clear dominance hierarchies and alpha males have preferential mating access to females, but cannot always monopolize all females (red colobus, Struhsaker and Leland 1979, Struhsaker and Pope 1991, Starin 1994, Hanuman langurs: Borries and Koenig 2000, Launhardt et al. 2001; guereza, Harris and Monfort 2003). Group size in both one- and multi-male groups is surprisingly similar, although both vary and can include up to

15 adult females (Newton 1987, Sterck and van Hooff 2000, Kirkpatrick 2011). While some multi-male groups are stable over time, many are suggested to be transitional. Intra-group male contests can be sudden or gradual, but often result in one-male groups; where a resident male is either replaced by a maturing son or a new male (Kirkpatrick 2011). Natal multi-male groups often become age-graded (Thomas's leaf monkey, Steenbeek et al. 2000) and young adult males rarely replace their fathers as the sexually active male (Gurmaya 1986, Steenbeek et al. 2000) and often split, resulting in one-male groups (Nilgiri langur, Hohmann 1989). Most knowledge on stable multi-male groups comes from Hanuman langurs, where there are up to 5 adult males in the group, and males form dominance hierarchies that determine access to receptive females (Borries et al. 1999a). Immigrant males are often former residents of adjacent groups (Borries et al. 1999b) and while they may achieve all ranks, low rank may promote some males to transfer (Borries 2000). Thus, in addition to births and deaths, group changes in colobines appear to be driven by reproductive strategies, including both male competition and female choice. While males compete for access to females, females can choose to either remain or transfer (Kirkpatrick 2011). Intergroup relations appear to be mediated by both males and females and are not necessarily based solely on food defense (resource defense polygyny; Thomas's leaf monkey, Wich et al. 2002 a,b; guereza, Fashing 2001, Harris 2006). Intergroup encounters may facilitate female transfer (e.g., snub-nosed monkeys, Kirkpatrick 1998) and male-male aggression between groups or against new males serves to defend females (female defense polygyny), which has been observed in several colobine species (capped leaf monkey, Stanford 1991a; Thomas's leaf monkey,

Steenbeek et al. 2000, Wich et al. 2002b, Wich and Sterck 2007; king colobus, Korstjens et al. 2002)

Dominance interactions

Despite earlier suggestions (Wrangham 1980, Sterck et al. 1997), recent studies suggest that female colobines compete over food resources, have agonistic relationships, and display despotic dominance hierarchies (Hanuman langurs, Hrdy and Hrdy 1976, Borries et al. 1991, Borries 1993, Koenig 2000, Lu et al. 2008; Thomas's leaf monkey, Sterck and Steenbeek 1997; king colobus, Korstjens et al. 2002; Phayre's leaf monkey, Koenig et al. 2004a). However, unlike stable matrilineal hierarchies in cercopithecine females, dominance hierarchies are often individualistic (not based on kinship or coalition formation) and (inversely) age-graded, with frequent ranks changes (Hanuman, Borries et al. 1991; Phayre's leaf monkeys, Koenig et al. 2004a; guereza, Dunbar and Dunbar 1976; Hanuman langur, Borries 1993, Borries et al. 1991, Koenig 2000; king colobus, Korstjens et al. 2002; ursine colobus, Saj et al. 2007). There is also evidence linking dominance rank to access to food and female fitness. High-ranking female Hanuman langurs are in better body condition (Koenig 2000), ingest more food (Borries 1993), conceive earlier (Koenig et al. 1997), and more often (Borries et al. 1991) compared to low-ranking females. Observations of Thomas's leaf monkeys, on the other hand, have failed to show any influence of female dominance rank on time spent feeding, feeding intake, or reproductive success (Sterck 1995, Sterck et al. 1997). Thus, further studies exploring the impact of female dominance relationships on nutritional condition and reproduction are needed.

Life history

Colobine life history has generally been reported as “fast”, with females giving birth at a younger age, having more offspring over the lifespan, and living shorter lives compared to frugivorous primates of similar body size (Leigh 1994, Wich et al. 2007). However, recent studies have called this idea into question suggesting that colobines might have aspects of life history that are slower (e.g., gestation) compared to cercopithecines (Borries et al. 2011).

Colobine life histories are also influenced by nutritional factors. For instance, provisioning or food abundance are known accelerate age at first reproduction (reviewed in Sterck 2012), increase the probability of conception (e.g., *Rhinopithecus bieti*, Xiang and Sayers 2009; *Semnopithecus entellus*, Koenig et al. 1997; *Trachypithecus leucocephalus*, Jin et al. 2009; *T. phayrei*, Borries and Koenig 2005, reviewed in Brockman and van Schaik 2005), reduce the length of interbirth intervals (e.g., Borries et al. 2001; reviewed in Sterck 2012), and accelerate weaning (white-headed black leaf monkey, Zhao et al. 2008b; silver leaf monkey, Shelmidine et al. 2009). In Hanuman langurs, the pace of life history, as measured by the frequency of births (IBI), is also influenced by social rank, an unsurprising result, given the association between rank and food intake / body condition.

Natal coloration

An interesting aspect of colobines that has received widespread attention is the fact that colobine infants are typically born with natal coloration that changes over the

first months of life (Treves 1997). Natal coats are found in all but one species of colobine (*N. narvatus*, Newton and Dunbar 1994). Most are conspicuous in color and mainly suggested to have evolved to attract female caretakers (infant handling or alloparenting, Hrdy 1976, but see Newton and Dunbar 1994, Treves 1997). Non-maternal caretakers (alloparents) are virtually ubiquitous in colobine monkeys, but there are some exceptions (e.g., red colobus, olive colobus; McKenna 1979; Newton and Dunbar 1994). In fact, red and olive colobus are believed to have darker natal coats due the lack of infant handling. However, the darker coat in Hanuman infants is more likely attributed to camouflage due to the high risks of predation and infanticide (Newton and Dunbar 1994). Infant handling is typical for females, and males may be more tolerant of infants but will alloparent on occasion and more often protect infants (Whitten 1987, Borries et al. 1999b; Kirkpatrick 2011, Sterck 2012). Nonetheless, in addition to improving maternal reproduction, allomothering may have important fitness benefits and costs for mothers, allomothers, and infants (Stanford 1992, Mitani and Watts 1997).

However, less is known about the direct relationship between maternal nutrition, energy transfer via lactation, and early infant development. It remains unclear whether speed of natal color change is a direct consequence of differences in the amount and quality of milk and whether this correlates with body mass of infants. However, several studies strongly support an effect of maternal body mass or fatness on growth rates of infants in both captive as well as wild populations of primates and other mammals (Johnson 2003, Altmann and Alberts 2005, Vervaecke et al. 2005, Hinde et al. 2009, Landete-Castillejos et al. 2010). Thus, it is likely that there are developmental implications for skin and pelage variables (Sumner and Mollon 2003, Bradley and

Mundy 2008). While some previous studies indicated that pelage chromaticities do not change much with the environment or the diet (captive versus wild; Sumner and Mollon 2003), other studies point to the importance of both genetic and environmental influences for the development of coat color (Caro 2005, Bradley and Mundy 2008). While the transition from natal to adult pelage is likely genetically pre-determined, the speed of melanin-based hair color change could also reflect nutritional condition or hormone levels. If and how diet and nutrition directly influence melanin pigmentation in primates is still largely unknown (Bradley and Mundy 2008). In general, it seems clear that access to adequate dietary nutrients can influence pigmentation in birds (Baker and Parker 1979) and mammals (Mundy et al. 1998, West and Packer 2002), which likely indicates that gene expression is sensitive to nutritional status (Roulin 2009). Thus, any variation in natal color change resulting from different maternal nutritional conditions could indicate an environmental influence in the transition from natal to adult coloration.

Phayre's leaf monkeys

Phayre's leaf monkeys (*Trachypithecus phayrei*) are an Asian colobine that occur in eastern Bangladesh, southwestern China, northeastern India, Lao PDR, Myanmar, Thailand (north of the peninsular zone) and northern Vietnam (Groves 2001). The species prefers primary and secondary evergreen and semi-evergreen forest, mixed moist deciduous forest, but is also found in bamboo-dominated areas, light woodlands, near tea plantations and in limestone forest (Nadler et al. 2005, 2007). The species is listed under the IUCN Red List as endangered ((EN) Criteria: A2cd; CITES Appendix II, IUCN 2013) as it has undergone a decline of more than 50% over the last three generations due to a combination of habitat loss and hunting (Bleisch et al. 2008). *T. phayrei* is recognized by IUCN to include three subspecies (*T. p. phayrei, T. p. crepuscula* and *T. p. shanicus*).

The study subspecies, *T. p. crepusculus*, occurs in southwestern China (central, southern and southwestern Yunnan, with the Salween River as its western boundary), Lao PDR, Myanmar (north of the peninsular zone south of the range of *T. p. phayrei* and west to the coast of the Bay of Bengal), northern Vietnam, and Thailand (north of the peninsular zone and range of *T. obscurus*) (Groves 2001). While originally described as a distinct species (*Pithecus crepuscula*, Eliot 1909), the taxon has been traditionally recognized as a subspecies of *T. phayrei* because of similar coloration (Napier and Napier 1967, Corbet and Hill 1992, Groves 2001) and recent molecular data suggest that it is a distinct species resulting in introgression or ancestral hybridization between two species groups (*T. obscurus* and *T. francoisi* groups; Geissman et al. 2004, Roos et al. 2007). Roos and colleagues found a distinct clustering of the Indochinese grey langur (*T. crepusculus*) with a distribution in northern Vietnam, southernmost China, Laos and central and northwest Thailand (Roos et al. 2007). While systematic classification for the population Phu Khieo Wildlife Sanctuary is underway (unpublished), the taxon is phenotypically distinguished by its light coat coloration, light eyerings, and depigmented skin over its lips (Groves 2001).

Overall, the species is reported to have a serious ongoing global decline due to hunting (for traditional medicine and bushmeat) and habitat disturbance, although the wild populations in Thailand are some of the best protected. Only two field studies have been conducted on Phayre’s leaf monkeys, including one in Tripura, India (*T. p. phayrei*, Gupta and Kumar 1994) and another long-term study on *T. p. crepusculus* in Phu Khieo Wildlife Sanctuary, Thailand (Borries et al. 2002, Koenig et al. 2004a, Borries et al. 2008, Koenig and Borries 2012).

Research at Phu Khieo Wildlife Sanctuary (PKWS) has been part of a long-term study established in October 2000 (by Andreas Koenig and Carola Borries), primarily concentrating on a wild population of Phayre's leaf monkeys (*T. p. crepusculus*) and I was active in the project since the establishment. From 2000-2009, baseline densities were established and four groups were habituated for behavioral studies. A demographic database was established for known individuals and research topics have included feeding ecology (Koenig et al. 2004b), dispersal (Borries et al. 2004, Koenig and Borries 2012), female social relationships (Koenig et al. 2004a, Larney, unpublished), infant handling and reciprocity (Larney, unpublished), male-infant relationships (Koenig et al., 2009), endrocrinology and reproduction (Lu 2009, Lu et al. 2012), factors shaping female fitness (Borries et al. 2008), and ontogyny in juveniles (Ossi, unpublished). The present study contributes to the collaborative project in establishing standardized collection of genetic samples and monitoring of both nutritional condition and early infant developmet.

Thus far, results from PKWS have shown that density estimates for this population are approximately 1.1 groups/ km^2, 16 individuals/ group and 20.1 individuals/ km^2 based on home range size and overlap (Hassel-Finnegan et al. 2008). Phayre's females frequently disperse (Borries et al. 2004) and may either leave or join groups with unweaned offspring (Larney, personal observation, Koenig and Borries 2012), while males either mature to breed in their natal group or leave to form new groups (Koenig and Borries 2012). However, it still is uncertain how groups are genetically structured and to what extent male reproductive skew and within and between group relatendess influence dispersal patterns.

Social organization varies from one-male to multi-male, with up to five adult males and 12 adult females (Borries et al. 2008, Koenig and Borries 2012). While female agonism is relatively infrequent and mostly consists of displacements over food, females form linear dominance hierarchies that are potentially age-inversed (Koenig et al. 2004). Initial results suggest some influence on food availability on female reproduction as conceptions peak related to food availability (Borries et al. 2005) and are more likely when females are in good physical condition (Lu et al. 2011). In addition, larger group size appears to delay infant development and weaning, and result in lower reproductive rates (Borries et al. 2011, Chapter 5). The interbirth interval after a surviving offspring is approximately two years on average (Borries et al. 2008) and births occur throughout the year, although there is a birth peak from November to April (Borries et al. 2011, Chapter 5). Infants that are born with conspicuous natal coats and infant handling is common, although infanticide has never been observed in this population. Nontheless, it is still unclear how social effects, such as kin-biased behaviors, group size, and rank may influence female nutrition and reproduction and if and how these maternal effects may continue to influence early infant development and ultimately female reproductive success.

Female dispersal and variability of group composition make Phayre’s leaf monkeys at Phu Khieo Wildlife Sanctuary an interesting species and population in which to carry out a study on genetic structure and reproduction. In addition, variability in group size, female dominance relations, nutrition and infant development make this an even more ideal location to combine further influences of social structure on female reproduction and early infant development.

Chapter Outline

This dissertation addressed three main goals: (1) to determine how groups are genetically structured and by what means, (2) to assess what influence, if any, kinship and familiarity have on female dispersal decisions and success at reproducing, and (3) to explore if nutritional and social maternal effects influence infant development after a female reproduces successfully.

In the following section, I outline the major objectives of each thesis chapter, providing a brief background on previous studies and hypotheses where relevant, although more extensive details will be provided in the chapters themselves. Note that while I am the primary author, all thesis chapters were collaborative efforts with coauthors that either contributed data or provided valuable ideas in the design of the study and/ or the interpretation of the results. Thus, I will use the pronoun “we” in subsequent chapters.

Chapter Two

In Chapter 2, we focus on the methodology in developing and screening polymorphic microsatellite markers for the endangered Phayre’s leaf monkeys (*Trachypithecus phayrei crepusculus*) from Phu Khieo Wildlife Sanctuary, northeastern Thailand using DNA extracted from feces. We present results from intensive screening of both novel and existing microsatellite primers using low-quality DNA extracted from feces. We characterize variation in up to 60 adult individuals from a wild population at Phu Khieo Wildlife Sanctuary, northeastern Thailand and present a panel of highly variable markers that genotyped consistently and accurately and are useful for examining population structure, dispersal, and kinship in the Phu Khieo population and can also serve as a useful resource for intra- and interspecific molecular studies on other Asian leaf monkeys.

Chapter Three

Genetic relatedness is considered a principle characteristic driving the structure of social groups and suggested to have direct influences on ecological and social contexts in gregarious primates (Wrangham 1980, van Schaik 1989, Isbell 1991, Moore 1992, Sterck et al. 1997). Chapter 3 describes the results of a molecular study of genetic variation, population structure and relatedness of Phayre's leaf monkeys in Phu Khieo Wildlife Sanctuary. Previous behavioral studies suggested female-biased dispersal (Borries et al. 2004), but in at least two cases males have also been observed to leave and form new groups and one male was observed to (re-)enter an established group (Koenig and Borries 2012), while other males have disappeared. While this population was under behavioral observation from 2001-2009, the use of genetic data in this study allows the potential to detect rare dispersal events by either sex, which may not have been directly observed and gain insight into how male reproductive skew may influence genetic structuring (Di Fiore 2003, Lawson Handley and Perrin 2007). Thus, we explored whether there is molecular evidence of population structure and specifically sex-biased dispersal in *T. p. crepusculus*. Following behavioral observations, we would expect to find genetic verification of female-biased dispersal. In particular, if there is greater male philopatry and female-biased dispersal in the population sampled, we would predict the following:

1. Average relatedness (R) among adult males within social groups should be greater than among adult females.
2. Adult males should have more adult same-sex kin within social groups than adult females.
3. Males should have a significantly higher average inbreeding coefficient (F_{IS}) than females.
4. Males should have significantly higher genetic differentiation (F_{ST}) among groups than females.
5. Males should have a significantly higher likelihood (mAIc) that their genotype originated in the group sampled versus other groups.
6. Males should have a significantly lower variance of assignment indices (vAIc) than females, indicating that females, rather than males, contain a greater mix of residents as well as immigrants from other social groups.

Chapter Four

Genetic relationships are an important factor in driving both proximate and ultimate causes of dispersal in animals (overview in Lawson Handley and Perrin 2007, Long et al. 2008). Although one of the most widespread factors influencing dispersal decisions is to avoid inbreeding (Pusey and Wolf 1996, Gandon 1999, Roze and Rousset 2003, Lawson Handley and Perrin 2007, Lukas and Clutton-Brock 2011), additional circumstances including relatedness to same-sex conspecifics is also a fundamental factor to consider as it may influence who disperses, how, and to where, as well as provide further insight into contextual variation between natal and secondary dispersers. There have been several theories presented to explain dispersal decisions dependent on kin relationships of both sexes in a group, including kin competition, kin cooperation, and inbreeding avoidance (Murray 1967, Hamilton and May 1977, Moore and Ali 1984, Pusey and Wolf 1996, Gandon and Michalakis 2001, Ronce et al. 2001, Bowler and Benton 2005, Lawson Handley and Perrin 2007, Long et al. 2008). However, further information from wild populations and female dispersal species, in particular, are lacking. In addition, how dispersal ultimately contributes to life history strategies such as reproductive success is critical to understanding the evolution of individual dispersal decisions.

Thus, Chapter 4 aims to understand the genetic factors influencing female dispersal decisions and reproductive success in wild Phayre's leaf monkeys. Since dispersal decisions may differ depending on a female's reproductive condition and relatedness to other females in the group, we consider the following categories for both disappearances and immigrations: (a) natal dispersal, (b) pre-breeding dispersal (non-natal juvenile or nulliparous female) and (c) breeding dispersal (all parous females) in relation to male and female relatives. We explore disappearances and emigrations and how relatedness affects a female's decision to leave, and more specifically whether inbreeding avoidance guides dispersal. If so, we would expect that females are more likely to leave with the presence of related males who are at or near the age of reproduction. To explore the possibility of non-random dispersal and potential for female kin associations, we were interested to where and why females immigrate in relation to both male and female relatedness. In addition, we explored the duration of time a female spent in a group (temporary visits versus stays of over 90 days) in relation to success at reproducing. If we come from the perspective of relatedness (inbreeding avoidance and kin-biased behaviors), we would expect (1) that females both leave and go into groups with unrelated males, (2) that the presence of female kin influences a female's decision to settle in a group, which could be guided by either kin cooperation or kin competition, and (3) that female reproductive success would be increased with fewer male relatives and more female relatives in groups. In the latter case, females should be attracted to groups with kin, because kin could make good allies if indeed individuals have the ability and opportunity to recognize their relatives as kin. However, if competition for group membership is strong or the costs of dispersal are less than remaining in a group with same-sexed kin, females should avoid groups with kin to avoid the costs of kin competition.

Chapter Five

Females may influence growth, maturation, and reproduction of their offspring in various ways, but primarily through nutrition, behavioral or physiological mechanisms, or social effects such as group size or dominance rank (see summary in Maestripieri and Mateo 2009). Chapter 5 explores maternal effects on infant development including the influence of group size, rank, and maternal nutritional condition on infant development over the first six months of life in Phayre's leaf monkeys. In the population under study, group size effects on reproductive rates have been documented (Borries et al. 2008) and females form linear dominance hierarchies with food being the most frequently contested resource (Koenig et al. 2004a), making it likely that maternal nutritional effects are present. As in most species in the genus *Trachypithecus,* Phayre's leaf monkey infants are born with light skin and nails and a flamboyant orange natal coat (Treves 1997). Following birth, the skin and coat color change gradually to gray over a period of 5-6 months (Treves 1997). Although the color change is likely genetically pre-determined, environmental influences on the timing of color change are known and gene expression can be affected by nutrition (Caro 2005, Roulin 2009). Thus, skin and coat color change could provide measurable developmental landmarks susceptible to maternal effects.

In Chapter 5, we present data based on a non-invasive assessment of maternal condition and a novel way to measure infant developmental landmarks in the wild. We first present results on the interrelationships between group size, rank, and maternal condition. Given that there is evidence for within-group scramble competition in this population (Borries et al. 2008) and most agonistic interactions within groups are over food (Koenig et al. 2004a), we predicted that females in smaller groups and females of higher rank should be in a better physical condition. Enhanced maternal nutritional conditions should lead to faster offspring development in the first months during infant dependency (Altmann and Alberts 2005). Consequently, we expected that infants in smaller groups, from mothers with good physical condition and of high rank to develop faster than infants in larger groups, from mothers with poor physical condition and of low rank.

Chapter Six

The chapters in this dissertation are closely integrated despite being presented as independent papers. Thus, the concluding chapter offers a synthesis of these results and provides direction for future research.

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Chapter 2

Identification and characterization of microsatellite markers for endangered Phayre's leaf monkeys using fecal DNA

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ABSTRACT

We identify polymorphic microsatellite markers for endangered Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*) based on results from screening both novel (N = 8) and established (N = 49) loci using DNA extracted from feces. We characterize variation in up to 60 adult individuals from a wild population at Phu Khieo Wildlife Sanctuary, northeastern Thailand, using a panel of 18 highly variable markers that genotyped consistently and accurately. Allelic diversity ranged from 5-14 alleles per locus, with expected heterozygosities ranging from 0.679-0.884. The high polymorphism and exclusionary power for identifying parentage provided by this panel are useful for examining population structure, dispersal, and kinship in the Phu Khieo population and can serve as a useful resource for intra- and interspecific molecular studies on other Asian leaf monkeys.

PRIMER NOTE

Molecular techniques are increasingly used in studies of primate phylogeny, population genetics, and behavioral ecology (Di Fiore 2003). Molecular studies of Asian leaf monkeys have largely focused on large-scale phylogenetic questions (e.g., Ting et al. 2006), while only a few (e.g., Launhardt et al. 2001, Sun et al. 2010, Yan 2012) have addressed population-level issues. One possible reason is that the identification and screening of sufficiently variable loci (e.g., microsatellites) for population-level studies is a labor- and cost-intensive process. The situation is particularly challenging when animals cannot be immobilized and lower-quality, non-invasive samples, e.g., feces, are the DNA source, which increases the potential for inaccurate genotyping (Taberlet et al. 1996, Monteiro et al. 1997). Here, we characterize a suite of polymorphic microsatellite markers for a population of endangered Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*; Groves 2001, Bleisch et al. 2008) that can be reliably scored from low-quality samples and that should be useful for group and population level genetic analyses of other Asian leaf monkeys as well.

We collected up to 5 g of fresh feces per individual from a wild population of Phayre's leaf monkeys at Phu Khieo Wildlife Sanctuary, northeastern Thailand. Samples were preserved dry using silica-based protocols (Wasser et al. 1997, Nsubuga et al. 2004) and were stored at ambient temperature until transferred to the laboratory (stored at 4-10 °C). DNA was extracted from these samples using QIAmp™ DNA Stool Mini Kits following manufacturer's protocols with the following modifications: i) the samples were initially left to lyse in ASL buffer at room temperature for 12-24 hours on a rocker, ii) the 70° proteinase K digestion stage was extended from 10 to 30 minutes, and iii) the DNA was eluted in 75-150 µL of AE buffer. Fecal extractions resulted in genomic DNA from a total of 141 individuals (Chapter 3).

Using the software MSAT Commander (Faircloth 2008), we screened a roughly 200 kB contig from the *Colobus* genome (NCBI, GenBank accession No. AC175372), for short tandem repeats (di and tetra-nucleotide motifs) for regions of approximately 20 base pairs regions, ranking the 200 bases before and after these microsatellite regions for primer suitability. Possible amplification primers were identified for these sequences using the program Primer 3 v4.0, included in MSAT Commander (Faircloth 2008). Nine markers were designed for screening using a high quality DNA sample (derived from blood of the closely-related *Trachypithecus obscurus*, Ting et al. 2006) and up to six *T. phayrei* fecal samples. Initial PCR reactions for screening were conducted in a 10 µl total volume consisting of 1 µL of template DNA, 0.625 x PCR Buffer, 1 mM dNTPs, 1.875 mM $MgCl_2$, 0.048 µM of each primer, 0.05 units/µL Amplitaq™ Gold (Perkin-Elmer) and 1 µg/µl BSA with the following protocol: 94°C for 5 min, 40 cycles at 94°C for 45 s, 54°C for 90 s and a final extension of 72°C for 7 min. PCR products were electrophoresed on 1-3% agarose gels and stained with EtBr to determine amplification success, size and variability. We selected 8 of the primer pairs to fluorescently label (either with 5' 6-FAM or HEX) and further optimize and genotype through multiplex PCR reactions (see below). We also screened 49 established Human MapPair™ loci (Resource Genetics; 5'-labelled with HEX, 6-FAM, NED or TET) using similar procedures (Table 2.1).

Genotyping PCR reactions were conducted using Qiagen™ Multiplex PCR Kits following the manufacturers' suggested concentrations (but in 1/5 the recommended total volume, i.e., in 10 μl reactions) and thermal cycling conditions. Annealing temperatures for nine loci were adjusted to optimize amplification, and primer pairs were multiplexed when possible (Table 2.1). Standard precautionary measures were used to minimize possible contamination, including i) conducting extractions and PCR reactions in dead air or laminar flow hoods, ii) using multiple negative controls (water) during extraction and genotyping, iii) simultaneously genotyping a reference human sample, iv) using a multiple tubes approach and replicating each genotype 2-7 times (Taberlet et al. 1996) and v) verifying allele-sharing from known mother-offspring pairs. PCR products were electrophoresed with a labeled size standard (GeneScan ROX-500) on an ABI 3730 Automated DNA Analysis System, and alleles were sized using GeneMapper Software v3.7.

Of the 57 microsatellite loci screened, 72% showed variability (≥ 2 alleles) in this population, including six of the novel loci (Table 2.1). Certain polymorphic loci (e.g., D7S817, D10S611) were excluded from our final panel (Table 2.2) due to inconsistent genotypes (indicating allelic dropout or potential null alleles). Additional markers (e.g., C2, C19, D3S1238, D4S111, Fesps) genotyped successfully overall, but were not included in the panel due to the comparatively lower levels of heterozygosity ($H_o < 0.6$) and/or polymorphism (< 5 alleles).

In Table 2.2, we present characteristics of a panel of 18 polymorphic microsatellite markers that we genotyped in up to 60 adult Phayre’s leaf monkeys. Overall, this panel of loci shows high heterozygosity per locus (mean $H_o = 0.833$) as well as variation (mean number of alleles = 8.63), and yields a high expected exclusionary power for parentage analysis (>0.999 with single parent; Peakall and Smouse 2006).

Genotype frequencies at three of the loci showed significant deviation from Hardy-Weinberg expectations at the population level, but not within sampled social groups (see details in Chapter 3).

The high level of variation of this suite of loci and the proven efficacy of using fecal samples as a DNA source will allow us to further investigate the Phu Khieo population, which has been a focus of a long-term study since 2000 (Koenig and Borries 2012). Molecular studies will be essential for addressing questions related to population structure, dispersal, and patterns of social interactions. Comparisons of genetic variation between existing *T. phayrei* populations could also be applied to conservation management strategies as well as phylogenetic and taxonomic questions (e.g., Geissmann et al. 2004, Liedigk et al. 2009). We expect that this panel will also serve as a useful resource for future molecular studies within and between other Asian colobines.

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Table 2.1 Summary of microsatellite loci screened for *T. p. crepusculus* (* indicates novel loci designed in this study)

Locus	Primer Sequence (5'-3')	Motif	T_a (°C)	Multi	N	K	Size Range (bp)		Marker Ref.
							T. phayrei	**Product**	
*C2	F: GAGAATGTGCCACTGTACTCCA R: ACTGGCTCTGAAACTCACCAAT	DI	56	1	143	2	271-275	277	AC166004
*C7	F: GAGGCAGGAAAATCACTTGAAC R: CCAGCTCCAAAACCTATGATCT	DI	55		5	4	292-298	234	AC163238
*C11	F: GAGCTCAGGAGTTTGAGACCAG R: TGACAGAGCAAGACTCCGTAAA	MONO	54		5	1	201	209	AC174629
*C16	F: CAGGTCACTGCACTCCAATCT R: AATGCCTTTCACCAAATTTCAG	TETRA	56	1	143	8	200-232	224	AC183706
*C17	F: CCCCAGGACCCTAGAACTAATC R: CATACTGGTGCAACTTCTTCCA		55		5	4		268	AC165191
*C19	F: TCTGAGCACTCTGGATTGTAGC R: ATCTCTGCACGCTTCACTTCTT	TETRA	54	2	143	7	220-248	205	AC153315
*C20	F: CATCCAAATGTTATCCGTTTT R: GACCACCAAGACTCCAGCTATC	DI	54	2	143	2	125-144	147	AC153314
*C21	F: AAGAAGGCTCCTCTCTGGTACA R: ACTGTAGTGCGATGCCTTCATA	MONO	54		7	1	187	185	AC152018
D1S207	F: CACTTCTCCTTGAATCGCTT R: GCAAGTCCTGTTCCAAGTCT	DI	55	8	141	12	132-155	142-170	GDB:188004
D1S533	F: CATCCCCCCCAAAAAATATA R: TTGCTAATCAAATAACAATGGG	TETRA	55		7	NA	--	193-225	GDB:686415
D1S548	F: GAACTCATTGGCAAAAGGAA R: GCCTCTTTGTTGCAGTGATT	TETRA	55		141	9	174-210	148-172	GDB:689691
D1S550	F: CCTGTTGCCACCTACAAAAG R: TAAGTTAGTTCAAATTCATCAGTGC	TETRA	55			1/NA		169-189	GDB:686748
D1S1665	F: TAAGTAAGTTCAAATTCATCAGTGC R: TTCCAAGCTTCACAGTGTCA	TETRA	55		59	5	142-163	229	GDB:685218
D2S119	F: CTTGGGGAACAGAGGTCATT R: GAGAATCCCTCAATTTCTTTGGA	DI	55		7	4	202-224	214-232	GDB:187933
D2S442	F: AAGGGAAGGAGCATAGCAAC R: GATTTGGTAGATAGACAGATGTGA	TETRA	55		55	10	197-244	196-208	GDB:686916
D2S1326	F: AGACAGTCAAGAATAACTGCCC	TETRA	55		3	2	215-219	232-268	GDB:684564

	R: CTGTGGCTCAAAAGCTGAAT								
D2S1399	F: CATTGGTCCAGGTAAACTGC R: TTCACAAGGTTCCACAAGGT	TETRA	55	4	143	12	162-213	144	GDB:686016
D3S1238	F: TGAGACCCTGTCTCTGAAAC R: TGTATGGGCTCTTGAAATTG	DI	55	5	143	2	116-118	118-146	GDB:186377
D3S1766	F: ACCACATGAGCCAATTCTGT R: ACCCAATTATGGTGTTGTTACC	TETRA	55	5	141	9	196-234	208-232	GDB:686805
D4S111	F: TTTCAGCCTCTATTTACCCAGCC R: CATTTTCCTTATTTCTGTTGCTTCC	DI	55	3	129	9	155-179		
D4S243	F: TCAGTCTCTCTTTCTCCTTGCA R: TAGGAGCCTGTGGTCCTGTT	TETRA	55	5	130	7	147-172	173	GDB:182214
D4S1652	F: AATCCCTGGGTACATTATATTTG R: CAGACATTCTTTATTCTTTACCTCC	TETRA	55			NA	--	136-148	GDB:686709
D4S2408	F: AATAAACTTCAACTTCAATTCATCC R: AGGTAAAGGCTCTTCTTGGC	TETRA	55		47	6	197-221	281	GDB:684549
D5S111	F: GGCATCATTTTAGAAGGAAAT R: ACATTTGTTCAGGACCAAAG	DI	55					167-171	GDB:178520
D5S117	F: TGTCTCCTGCTGAGAATAG R: TAATATCCAAACCACAAAGGT	DI	55		33	1	133	147-163	GDB:177306
D5S1457	F: TAGGTTCTGGGCATGTCTGT R: TGCTTGGCACACTTCAGG	TETRA	55		142	6	108-128	97-127	GDB:684402
D5S1470	F: CATGCACAGTGTGTTTACTGG R: TAGGATTTTACTATATTCCCCAGG	TETRA	55		4	1	149	197	GDB:685680
D6S311	F: ATGTCCTCATTGGTGTTGTG R: GATTCAGAGCCCAGGAAGAT	DI	55		24	3	219-225	230-176	GDB:188611
D6S474	F: TGTACAAAAGCCTATTTAGTCAGG R: CATGTGAGCCAATTCCTCT	TETRA	55		8	4	109-225	165-170	GDB:686577
D6S1056	F: ACAAGAACAGCATGGGGTAA R: CCTGGATCATGAATTGCTAT	TETRA	55					250	GDB:685479
D6S1280	F: CTGAATTTAGTCAGGGGTTCC R: TCCATCACATGAGCAATTTC	TETRA	55	4	141	6	159-179	171	GDB:456008
D7S503	F: ACTTGGAGTAATGGGAGCAG R: GTCCCTGAAAACCTTTAATCAG	DI	55		15	4	307-321	148-180	GDB:188277
D7S817	F: TTGGGACCTCTTATTTTCCA R: GGGTTCTGCAGAGAAACAGA	TETRA	55	8	128	9	171-211	157-177	GDB:686505
D7S1817	F: CAAATTAATGGCAAAAACTGC R: CCCCCCATTGAGGTTATTAC	TETRA	55	9	141	10	117-151	122	GDB:684423

D8S164	F: GATCATGTGAGTTAATACTTAAT R: TCAGCTGCCTGTATTACTCA	DI	55		4	NA	--	165-199	GDB:180560
D8S165	F: ACAAGAGCACATTTAGTCAG R: AGCTTCATTTTTCCCTCTAG	DI	55		14	3	152-158	138-152	GDB:180699
D8S260	F: AGGCTTGCCAGATAAGGTTG R: GCTGAAGGCTGTTCTATGGA	DI	55	3	117	4	177-185	187-213	GDB:188000
D8S271	F: AGATGACCTGGATGAGAGTG R: AACAAACTTGCTTATGAGTGTTACT	DI	55		4	NA	--	257-271	GDB:188156
D8S536	F: AGCAAGACCCCACCACTACA R: AGCATAATACAGTTTGCANTTGTA	DI	55		4	2	169-173		GDB:199613
D10S611	F: CATACAGGAAACTGTGTAGTGC R: CTGTATTTATGTGTGTGGATGG	TETRA	55		19	8	143-156	152	GDB:208285
D10S676	F: GAGAACAGACCCCCAAATCT R: ATTTCAGTTTTACTATGTGCATGC	TETRA						175-199	GDB:686829
D10S1432	F: CAGTGGACACTAAACACAATCC R: TAGATTATCTAAATGGTGGATTTCC	TETRA	56	6		12	140-194	165-181	GDB:685833
D11S1366	F: GCTACAATGATAGGGAAATAATAGA R: GGTGGGATCCTTTGCTATTT	TETRA	55		4	1	223	241	GDB:686592
D11S2002	F: CATGGCCCTTCTTTTCATAG R: AATGAGGTCTTACTTTGTTGCC	TETRA	55	4	141	6	248-268	237	GDB:365242
D12S391	F: AACAGGATCAATGGATGCAT R: TGGCTTTTAGACCTGGACTG	TETRA						225-233	GDB:686475
D13S159	F: AGGCTGTGACTTTTAGGCCA R: CCAGGCCACTTTTGATCTGT	DI	55		15	4	307-321	169-203	GDB:188095
D13S160	F: CGGGTGATCTAAGGCTTCTA R: GGCAGAGATATGAGGCAAAA	DI	55		5	2	232-234	229-241	GDB:188101
D13S318	F: GTATGATTTATTTCAGGTTTGCA R: TTTGATTTCATTGTCTACTGACA	TETRA	55	9	MANY	9+	172-204	284	GDB:686760
D13S321	F: TACCAACATGTTCATTGTAGATAGA R: CATACACCTGTGGACCCATC	TETRA	55	5	141	8	170-198	202	GDB:686418
D14S51	F: GATTCTGCACCCCTAAATCC R: ATGCTCAATGAACAGCCTGA	MONO	55		5	1	125	131-149	GDB:191687
D14S306	F: AAAGCTACATCCAAATTAGGTAGG R: TGACAAAGAAACTAAAATGTCCC	TETRA	55	3	141	6	140-160	190-212	GDB:686652
D16S420	F: ATTTCCTGAGGTCTAAAGCACCC R: TTAGGCCCAGTCCACACTCAAG	DI	55		15	4	307-321	179-201	GDB:188484
D17S1290	F: GCCAACAGAGCAAGACTGTC	TETRA	55	3	141	14	149-218	199	GDB:364316

	R: GGAAACAGTTAAATGGCCAA								
D18S536	F: ATTATCACTGGTGTTAGTCCTCTG R: CACAGTTGTGTGAGCCAGTC	TETRA	55		4	3	161-173	146-170	GDB:686892
D19S714	F: ATGCCCTCTTCTGTCTCTCC R: GCAGAGAATCTGGACATGCT	TETRA	56	6	141	7	227-256	229	GDB:685410
D20S206	F: TCCATTATTCCCCTCAAACA R: GGTTTGCCATTCAGTTGAGA	TETRA	55		3	2	122-126	125	GDB:686433
Fesp	F: GGAAGATGGAGTGGCTGTTA R: CTCCAGCCTGGCGAAAGAAT	TETRA	55		48	6	129-145	143-163	Polymeropoulos MH et al. 1991

Motif = oligonucleotide repeat motif

Ta = annealing temperature

Multi = multiplex group

N = number of individuals genotyped

K = number of alleles per locus (NA = did not amplify well using fecal samples)

Table 2.2 Characteristics of 18 microsatellite loci best suited for genotyping DNA derived from fecal samples in a population of *T. p. crepusculus*

Primer	**Motif**	**N**	**K**	**Ho**	**He**
C16	TETRA	60	8	0.899	0.71
C19	TETRA	60	7	0.944	0.776
D1S207	DI	60	12	0.882	0.817
D1S548	TETRA	60	9	0.994	0.749
D1S1665	TETRA	59	5	0.655	0.635
D2S442	TETRA	55	10	0.85	0.821
D2S1399	TETRA	60	12	0.926	0.82
D3S1766	TETRA	60	9	0.9	0.806
D4S2408	TETRA	47	6	0.699	0.703
D5S1457	TETRA	60	6	0.855	0.775
D6S1280	TETRA	60	6	0.885	0.78
D7S1817	TETRA	60	10	0.872	0.795
D10S1432	TETRA	60	12	0.748	0.678
D11S2002	TETRA	60	6	0.84	0.715
D13S321	TETRA	60	8	0.8	0.777
D14S306	TETRA	60	6	0.887	0.73
D17S1290	TETRA	60	14	0.843	0.799
D19S714	TETRA	60	7	0.827	0.746

N: number of adult individuals genotyped

K: number of alleles per locus

Ho: Observed heterozygosity

He: Expected heterozygosity

Chapter 3

Dispersal and genetic structure of a wild population of Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*) in Phu Khieo Wildlife Sanctuary, Thailand

ABSTRACT

Dispersal and reproduction influence the genetic structure of social groups across space and time and both behavioral and molecular analysis can give important insight into group structure. Female dispersal in primates is comparatively rare and new insights are becoming available with research coupling genetic and demographic data. We describe the genetic structure and dispersal in Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*) using genotype data from 141 individuals in northeastern Thailand. We found support for female dispersal in this species, although genetic analysis also showed evidence for male-mediated gene flow in the population. However, direct observations confirmed frequent natal, pre-breeding and secondary female dispersal, while males were generally observed to stay within their natal group or neighboring range. Parentage analysis showed a slightly longer reproductive tenure in multi-male groups, but at a cost of sharing reproduction with other group males, resulting in mixed paternity such that similar aged animals may be unrelated. Although males had slightly lower average relatedness (11%) compared to females (13%), pointing towards a male bias in dispersal, the other measurements for genetic differentiation indicated no significant bias in dispersal by either sex. However, coupled with behavioral data, we find that long male tenure leads to female dispersal and gene flow, while male-mediated gene flow is through females secondarily dispersing (pregnant or with infants), extra-

group paternities and alternative forms of new group formation. While both sexes showed low levels of relatedness, networks of same-sexed relatives were present both within and between groups and could potentially indicate non-random dispersal and offer opportunities for kin cooperation among both sexes both within and between groups.

INTRODUCTION

Dispersal patterns, social structure, and individual reproductive success are considered predictive of genetic population substructure. Dispersal has important consequences for the genetic structure of a population because it mediates the movement of alleles within and between populations (Chepko-Sade and Halpin 1987, Clobert et al. 2001, Di Fiore 2003, 2009, Lawson Handley and Perrin 2007). For primate social groups, dispersal and reproductive strategies influence the structuring of genetic variation within and among social groups across space and time (Altmann et al. 1996, Gandon and Michalakis 2001, Vigilant et al. 2001, Di Fiore 2003, 2009, Clutton-Brock and Lukas 2012) and kin relationships influence patterns of cooperation and competition within and between groups (Greenwood 1980, Sterck et al. 1997, Silk 2002, 2007; but see Mitani et al. 2000, Langergraber et al. 2007)

Dispersal by individuals and subsequent reproduction results in the transfer of genes across a geographic landscape. Many taxa, especially birds and mammals, exhibit sex-biased dispersal patterns where males and females differ in their age at dispersal, dispersal distance, or other characteristics (for review see Lawson Handley and Perrin 2007). Complete bias in dispersal, where one sex remains exclusively philopatric, is rare in mammals but generally more common in birds and to some degree in primates (Pusey and Packer 1987, Greenwood 1980, Johnson and Gaines 1990, Lawson Handley and Perrin 2007, Lukas and Clutton-Brock 2011). In cercopithecine species, males typically emigrate from their natal group and females remain predominantly philopatric (Wrangham 1980, Melnick and Pearl 1987, Pusey and Packer 1987, Clutton-Brock 2009). However in several other primates, females are the predominant dispersers, or both sexes disperse but at varying distances or ages (Moore 1984, Pusey and Packer 1987, Pope 1992, Strier 1994, Nishimura 2003, Stokes et al. 2003, Di Fiore 2003, Bradley et al. 2004, Bradley et al. 2007, Douadi et al. 2007, Huck et al. 2007, Lawson-Handley and Perrin 2007, Morelli et al. 2009, Di Fiore 2009, Di Fiore et al. 2009, Clutton-Brock and Lukas 2012, Inoue et al. 2013).

Both males and females ultimately have the same goal of passing along their genes; however, since males and females differ in their reproductive investment and resource-holding constraints, the strategy may differ leading to diversified social systems across primates (Trivers 1972, Emlen and Oring 1977, Wrangham 1980, Smuts et al. 1987, Kappeler and van Schaik 2002, Strier 2011). Theoretical models for ultimate and proximate causes of dispersal, and particularly sex-biases in dispersal, invoke inbreeding avoidance (Packer 1979, Dobson 1982, Shields 1982, Waser et al. 1986, Pusey 1987, Clutton-Brock 1989, Gandon 1999, Lukas and Clutton-Brock 2011, Clutton-Brock and Lukas 2012) or kin selection arguments including local mate competition (Dobson 1982, Hamilton 1967, Moore and Ali 1984) and local resource competition (Clarke 1978, Greenwood 1980, 1983, Pusey and Packer 1987, Shields 1987). Primate socioecological models have built upon these models to explain complex social behavior including cooperative behavior and affiliative relationships, as well as patterns of female philopatry. Generally, these models predict that female primates should be philopatric when they would benefit by forming coalitions in response to competition for food resources (i.e., when food resources are distributed in high-quality patches and within-group or between-group contest competition for food resources is high). When food resources are low quality, scattered, or very large and contest competition is low, females may not need to form coalitions and may find it less costly to disperse (Wrangham 1980, Isbell 1991, Moore 1992, van Hooff and van Schaik 1992, van Schaik and Hörstermann 1994, van Schaik 1989, Sterck et al. 1997). However, more recently the idea of links between food distribution, competition and dispersal has been questioned (e.g., Koenig 2002, Thierry 2008, Koenig and Borries 2009, Clutton-Brock and Janson 2012, Clutton-Brock and Lukas 2012).

Even among the dispersing sex, same-sex matrilines or patrilines can develop over time if dispersal is a condition dependent tactic and if there are benefits to cooperating with same-sexed kin for either ecological (Wrangham 1980, Sterck et al. 1997) or reproductive resources (e.g., Pope 1990). Patterns of within group genetic relatedness may also be influenced if there is a high reproductive skew among males within a social groups, which results in cohorts of similarly aged individuals being more closely related to one another through common paternity than are animals of different ages (Pope 1990, Widdig et al. 2001, 2002, Lukas et al. 2005). Similarly, extra-group mating by either males or females can reduce the extent of genetic differentiation (i.e., levels of relatedness) between groups (Vigilant et al. 2001, Di Fiore 2009).

Nonetheless, genetic relatedness (and particularly nepotism, or kin-biased cooperative behaviors) is considered a principle characteristic driving the structure of social groups and suggested to have direct influences on ecological and social contexts in gregarious primates (Wrangham 1980, Isbell 1991, Moore 1992, van Schaik 1989, Sterck et al. 1997). However, dispersal events are often rare, especially due to the relatively long life histories of higher primates, and long-term studies are needed. In addition, behavioral observation of sexual behavior may not always be a clear indication of an individual's reproductive success, since sexual behavior does not always purely equate with conception and have genetic consequences and primate reproductive phases may span over the course of several years (e.g., Vigilant et al. 2001). In addition, skewed male reproductive success may influence average relatedness among resident males and females, as Seger (1977) suggested in one-male groups in relation to male tenure. Thus, advances in molecular primatology have been crucial in providing indirect means of characterizing the dispersal and reproductive behavior of individuals in addition to examining patterns of relatedness among animals both within and between groups (Di Fiore 2003, 2009, Di Fiore et al. 2009).

We describe the genetic variation, population structure and relatedness of Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*) from a continuous and well-protected population in Phu Khieo Wildlife Sanctuary located in northeastern Thailand. Previous behavioral studies on this population suggested female-biased dispersal (Borries et al. 2004). Females appear to disperse frequently (Chapter 4), but in at least two cases males have also been observed to leave and form new groups and one male was observed to (re-)enter an established group (Koenig and Borries 2012), while other males have disappeared. While this population was under behavioral observation from 2001-2009, the use of genetic data in this study also allows the potential to detect rare dispersal events by either sex, which may not have been directly observed (Di Fiore 2003, Lawson Handley and Perrin 2007). There have been few genetic studies of dispersal in primates, and only one other genetic study of dispersal in an Asian colobine (*Rhinopithecus roxellana*; Tan and Guo 2007, Zhao et al. 2008, Yao et al. 2011, Yan 2012).

In this study, we explored whether there is molecular evidence of population structure and specifically sex-biased dispersal in *T. p. crepusculus*. Following behavioral observations, we would expect to find genetic verification of female-biased dispersal. In particular, if there is greater male philopatry and female-biased dispersal in the population sampled, we would predict the following:

1. Average relatedness (R) among adult males within social groups should be greater than among adult females.
2. Adult males should have more adult same-sex kin within social groups than adult females.
3. Males should have a significantly higher average inbreeding coefficient (F_{IS}) than females.
4. Males should have significantly higher genetic differentiation (F_{ST}) among groups than females.
5. Males should have a significantly higher likelihood (mAIc) that their genotype originated in the group sampled versus other groups.
6. Males should have a significantly lower variance of assignment indices (vAIc) than females, indicating that females, rather than males, contain a greater mix of residents as well as immigrants from other social groups.

METHODS

Study site and data sampling protocol

This study was conducted on a wild population of Phayre’s leaf monkeys (*Trachypithecus phayrei crepusculus*) in Phu Khieo Wildlife Sanctuary (16°5’-35’ N, 101°20’-55’ E), Northeast Thailand (for detailed site description see Borries et al. 2002; Koenig and Borries 2012). The sanctuary consists of a relatively large continuous tract of mixed evergreen and dry dipterocarp forest (157,300 ha, 500-1,300 m asl; Figure 3.1). The sanctuary contains an intact predator community (Grassman et al. 2005) and 7 primate species (*Hylobates lar*, *Macaca arctoides*, *M. assemensis*, *M. leonina*, *M. mulatta*, *Nycticebus bengalensis*, and *T. phayrei*; Borries et al. 2002, Hassel-Finnegan et al. 2008). It remained unclear whether Indochinese luntungs (*T. germaini*) were also present.

Habituation of this population began in October 2000 and systematic demographic and behavioral observations were conducted from January 2001 through January 2009 in the main study site Huai Mai Sot Yai (16°27’N, 101°38’E; 1,300 ha, 100 km of trails, undisturbed habitat, 600-800 m.a.s.l., Figure 3.1). Based on home range size and overlap, density estimates for this species are approximately 1.1 groups per km^2, 16 individuals per group and 20.1 individuals per km^2 (Hassel-Finnegan et al. 2008). The population consists of both one and multi-male groups that vary in size from 6 to 33 individuals (Koenig and Borries 2012). Four habituated groups (PA, PB, PO, PS) have been the main focus of data collection. Focal groups varied in size and composition with an average of 19.48 individuals per group, including 1.95 adult males, 7.18 adult females, 4.68 subadults and juveniles and 5.68 infants (for more details see Koenig and Borries 2012, Chapter 4). Behavioral observations show female-biased dispersal (Borries et al. 2004, Chapter 4) and males either mature and breed in their natal group or leave to form new groups (Koenig and Borries 2012). Behavioral observation from 2000-2009 also allowed for identification of mother-offspring dyads within the focal groups, and the age of an individual was either determined by the exact date of birth or, for older individuals and many of the immigrants, we estimate age by comparing the size of the individual to individuals with known date of births. However, since data were combined across sampling years for genetic analyses, individuals were classified under two categories: (1) adult – including all adult and subadult individuals at the start of behavioral observations in a particular group in addition to all immigrating females and (2) non-adult – including all known natal offspring born into groups during the study (including uncertain females that were confirmed to be natal from parentage analysis). During population sampling of non-habituated groups, individuals were sexed when possible at the time of sample collection.

Fecal sample collection

Fresh fecal samples (ca. 5 g within a half hour of the time of defecation) were collected noninvasively from Phayre's individuals from 2002-2008, with intensive sampling during the primary field phase for my dissertation research (2004-2006). From 2002 to 2004, samples were stored using the one-step silica beads preservation method (Wasser et al. 1997) while samples collected from 2005 on were stored using the improved 2-step approach (Nsubuga et al. 2004) of collecting samples in 95% ethanol and then transferring the pellet, usually within 24 hours after collection, to a sterile Falcon ™ vile containing 3/4 silica desiccant. Samples were collected from most individuals in four adjacent habituated groups. At least three samples were collected from each individual whenever possible (e.g., individuals might have only come into a group temporarily or disappeared/ died before multiple or any sample could be taken) on different days and throughout different times of the year.

To provide additional information for population allele frequency estimates, unhabituated individuals were also targeted every month for 1-2 days during the primary field phase for dissertation research (2004-2006), primarily targeting neighboring groups within the main study area, in addition to opportunistic encounters (intergroup encounters) and fecal samples (from approximately 12-13 groups) were collected whenever possible. Samples were stored at ambient temperature in the field and then shipped to New York University's Molecular Anthropology Laboratory for analysis.

DNA template extraction

Genetic work was conducted at New York University's Molecular Anthropology Laboratory from 2006-2008. A total of 384 fecal samples were used for nuclear DNA extraction. When possible, multiple samples (from different days of collection) were targeted for extraction to confirm individual identification and control for misidentification or contamination at the time of fecal collection. At least two independent fecal samples (ideally collected by myself or two different field collectors on different days) were selected for extraction for each individual whenever possible. Extraction protocol followed Qiagen (QIAamp DNA Stool Mini Kit™) manufacturer's procedures with slight modifications, including: samples were allowed to initially lyse in ASL buffer for up to 24 hours in a rocker, increasing to 35 μL of proteinase K (20 mg/ml) prior to adding the supernatant and then placed in a thermoblock for 30 minutes, and a final elution in AE buffer between 75 to 200 ul and incubated at room temperature for 30 minutes (for further details see Chapter 2).

Nuclear DNA Genotyping

Following initial primer screening (Chapter 2), PCR reactions were conducted using Qiagen Multiplex Kits™ following the manufacturers protocols reduced to one-fifth the total recommended volume (10 μl reaction volumes rather than 50 μl; for additional details see Chapter 2). Each PCR reaction included a negative and human (E. Larney) control. Each sample was genotyped across at least 15 polymorphic nucleotide repeat microsatellite loci that were identified as informative for this species (Chapter 2). Primer pairs were fluorescently labeled (5' end of either the forward or reverse primer at each locus) and multiplexed when possible (for details see Chapter 2). Amplification conditions used a standard protocol on Bio-Rad thermal cyclers (94 °C for 2 min, 35 cycles of 94 °C for 30 s, 55 °C for 30 s, and 72 °C for 1 min, and a final extension at 72 °C for 5 min) with slight modifications for marker-specific optimization in terms of annealing temperature and number of cycles determined during primer optimization (see Chapter 2).

Amplified PCR products were separated using electrophoresis (ABI 3730 Automated DNA Analysis System). Alleles were sized relative to an internal size standard (ROX-500) using Gene Mapper software (Applied Biosystems) and binned by eye. Individuals were genotyped and scored using at least 2 replicates for heterozygotes and at least 7 replicates for homozygotes (Morin et al. 1994, Taberlett et al. 1996, Morin et al. 2001). In addition, known mother-offspring dyads were checked for allelic mismatch whenever possible. Due to volume limitations, some census samples were unable to be genotyped and scored reliably at all loci. Thus, some of individuals were discarded from further analyses; while for all others, we included only complete genotypes in the overall allele frequency and relatedness estimates.

Sexing

Confirmation of the sex of all individuals was important for determining the dispersal pattern. While most individuals were sexed at the time of collection, verification of sex of individuals, and especially population samples, was conducted following the protocol described in Di Fiore (2006) through multiplex amplification of shorter, nonhomologous regions of the X (amelogenin) and Y (SRY) chromosomes. All individuals were genetically sexed and all habituated individuals (n= 102) matched 100% in observed versus genetic sex classification and all population samples (n=39) were assigned for further analysis using the genetic sex.

Genetic Analyses

Data screening

Data were screened for scoring errors due to stuttering, and tested for homozygosity and small allele dominance, deviations from linkage disequilbrium, and evidence for null alleles using MICROCHECKER (van Oosterhout et al. 2004). Data were further tested for heterozygote deficiency (FI_S) and null alleles using CERVUS 3.0.3 (Marshall et al. 1998) and GENEPOP 3.4 (Raymond and Rousset 1995) employing the Markov chain method (Guo and Thompson 1992).

Discrimination of individuals

Unique multilocus genotypes were identified using the programs GenAlEx version 6.501 (Peakall and Smouse 2006) and CERVUS 3.0.3 (Marshall et al. 1998) in order to ensure that duplicate samples were not included in the analysis. Samples that had mismatches at up to two loci were re-examined for possible genotyping errors or allelic dropout or additional samples were extracted and re-run to confirm if a sample was potentially misidentified at the time of sample collection.

We calculated the probability of identity statistic $P_{(ID)}$, the probability that two different individuals drawn at random will share the same multilocus genotype at a given number of loci based on allele frequencies in the population (Peatkau and Strobeck 1994) using CERVUS 3.0.3 (Marshall et al. 1998). In addition, we also calculated a more conservative measure of $P_{(ID)}$, $P_{(ID\text{-}sibs)}$, or the probability that a pair of siblings will share the same genotype (Waits et al. 2001), to ensure that the suite of loci used could reliably discriminate related individuals.

Genetic variation

Data was further examined for genetic diversity, allelic richness and deviations from Hardy-Weinberg equilibrium using GENEPOP 3.4 (Raymond and Rousset 1995) and GenAlEx version 6.501 (Peakall and Smouse 2006). Data were tested both as a single population as well as by group and significance values were adjusted by Bonferroni correction (Rice 1989). Background population allele frequencies included only adult individuals and were calculated using CERVUS 3.0.3 (Marshall et al. 1998) and GenAlEx version 6.501 (Peakall and Smouse 2006). The robusticity of the suite of loci for estimating relatedness was tested with rarefaction analysis using the program RE_RAT (http://people.musc.edu/~schwaclh/; Altmann et al. 1996, de Ruiter and Geffen 1998).

Maternity and paternity

Parentage analyses (maternity and paternity) were conducted with the maximum likelihood method using CERVUS 3.0.3 (Marshall et al. 1998, Kalinowski et al. 2007) with alpha set to default parameters of 95% (strict) and 80% (relaxed) confidence. CERVUS uses simulations (with the true parent's identity set as known for each offspring) to evaluate the confidence in parentage assignments in relation to the most likely candidate parent by incorporating observed allele frequencies, the number of candidate parents, the proportion of candidate parents sampled and typed, and genotyping error due to potential contamination, allelic dropout, stutter, null alleles or human error. This program assigns each parent-offspring pair with a LOD score, which is derived by taking the natural log of the overall likelihood ratio for each parent-offspring pair. A LOD score of zero means that the candidate parent is equally likely to be the true parent as it is to not be the true parent. A negative LOD score indicates that the candidate parent is less likely to be the true parent than not the true parent, and more likely with a positive LOD score. Confidence values are calculated by comparing a distribution of simulated values to the difference between actual LOD scores for the two most-likely candidate parents. Thus, parentage analysis included a set of offspring, a set of parents (mothers or fathers), and a no true parent set. The proportion of parents sampled was set at 50% and 95%, with an 86% proportion of loci typed, 1% error rate, and minimum criteria of at least 10 loci typed. If the LOD score of the most likely candidate parent was high compared to simulated values, parentage was assigned. However, if the LOD score was 0, this means that the candidate parent is as equally likely as a random individual to be the true parent. Thus, candidates with the highest (positive) LOD score indicated the most likely mother or father to a particular offspring with 95% confidence.

While behavioral observation confirmed many of the mother-offspring relationships, maternity was conducted on all potential offspring (n=64) to confirm mothers of natal individuals born into the group or weaned and suspected to be natal (n=42), young adult and sub-adult females at the start of the study (n = 8) and immigrant females of unknown origin (n = 14). All adult females that were scored at 10 or more loci were considered as potential mothers (n=70). Maternity for females, in particular, can be used to determine mother-offspring relationships between females within and between groups to assist in explanations of group sub-structuring. All strict maternity assignments confirmed via both exclusion and by observed association between a female and a particular offspring were included as 'known' mothers in subsequent paternity analysis. For paternity analysis, all adult males from the population were included as potential sires to all immigrating females and juveniles, and LOD scores were calculated with and without the 'known' mothers genotype. Paternity estimates included a sample of 21 candidate males (all adult males plus one subadult male, Am5.1, that could have sired offspring towards the end of the study) and the same 64 potential offspring also included in the maternity analysis.

Pairwise relatedness

Dyadic (pairwise) relatedness was estimated for all possible dyads of individuals from the population using the regression based Queller and Goodnight (1989) relatedness estimator as implemented in GenAlEx version 6.501 (Peakall and Smouse 2006). Pairwise dyadic relatedness values are noted as “r-values” while average relatedness values across multiple dyads within a category are noted as “R” or average relatedness among multiple dyads. Confidence intervals and standard errors of average relatedness values were generated by jackknifing across loci. Standard deviations of estimates of average relatedness are used as these are independent of the sample size since standard errors are not informative for comparison between analyses of different samples sizes. All analyses were performed at the population level. The between-group analysis was performed for 5 groups (PA, PB, PS, PO and Census). Dyadic relatedness was ascertained for all individuals within the group and dyads were considered related at a reladedness values of either $r \geq 0.125$ – $r<0.25$ or $r \geq 0.25$. Average relatedness was distinguished within sexes (male and female) and demographic categories (adult and non-adult). I explored the average relatedness of (1) adults (males versus females) within and between groups, (2) adult individuals (male and female) within a group relative to the whole population, (3) of non-adults (males versus females) within and between groups, and (4) of non-adult individuals (male and female) within a group relative to the whole population.

Population structure and sex-biased dispersal

We used four tests for sex-biased dispersal using GenAlEx version 6.501 (Peakall and Smouse 2006) and FSTAT 2.9.3.2 (Goudet 1995, 2001), which are not only sensitive to the extent of the bias in dispersal seen between sexes but also to the sampling strategy (e.g., the number of populations/groups and individuals per population/group sampled as well as the genotypic variation in the animals (Goudet et al. 2002, Di Fiore 2009). Data analysis was conducted among sexes (male versus female) and demographic classes (adult and non-adult). We included all 20 adult males and 78 adult females from the entire population in these tests due to the difference in sample size between males and females, in addition to testing the 21 non-adult males and 22 non-adult females independently.

We first estimated the level of inbreeding (F_{IS}) or the mean reduction in heterozygosity of an individual due to non-random mating within a population. This inbreeding coefficient can range from -1.0 (all individuals heterozygous) to +1.0 (no observed heterozygotes) and is a measure of how well the genotype frequencies within the population match Hardy-Weinberg expectations (Hartl and Clark 1997). Positive F_{IS} values are expected for the dispersing sex due to a mixture of immigrants and residents at any one site. This hidden subdivision can lead to a heterozygote deficiency and a positive F_{IS} (i.e., Wahlund effect). In addition to comparing F_{IS} between male and female adults in the population, we also compared F_{IS} of same-sexed adults versus juveniles to explore inbreeding coefficient in relation to sex-biased gene flow (i.e., the adults of the dispersing sex will have higher F_{IS} value)

We also estimated gene flow/ genetic variation using Wright's fixation index (F_{ST}) or the mean reduction in heterozygosity of a subpopulation (groups relative to the total population) due to the genetic drift among subpopulations (groups). This value ranges from 0.0 (no differentiation) to 1.0 (complete differentiation where subpopulations are fixed for different alleles). The dispersing sex should have lower F_{ST} values because it expresses the proportion of the total genetic variance attributable to among-population differentiation (Hartl and Clark 1997). The dispersing sex should be less differentiated in its allelic frequencies than the more philopatric sex. Genetic structure (F_{ST}) of same-sexed adults was conducted to explore the genetic variation explained by subpopulation or group membership. Significance of pairwise F_{ST} values was calculated using permutation tests (N=1000) and Bonferroni corrected for multiple comparisons (Weir and Cockerham 1984).

We then estimated mean and variance for Assignment index (AI) for individuals in addition to comparing between sexes to explore which individuals (and sex) were more likely to be born in the sampled population versus immigrants. Allele frequencies at each locus (AIc) were then corrected for multilocus probabilities giving a corrected value for each individual (mAIc; Paetkau et al. 1995, Favre et al. 1997, Goudet et al. 2002). Resident individuals are expected have positive AIc values since the more philopatric sex's genotypes are more likely than average to occur in the sample. Members of the dispersing sex, on the other hand, are expected to have negative Alc values since immigrant genotypes are less likely to occur in a representative sample (Goudet et al. 2002). The mean Assignment Index should be higher in the more philopatric sex, while the variance of Alc (vAlc) should be higher in the dispersing sex, since the latter is expected to include dispersed and resident genotypes with both positive and negative values.

RESULTS

Descriptive statistics and unique individuals

Overall, 141 unique individuals from 384 fecal samples in which DNA template was extracted were included in this analysis (Table 3.1). Several independent samples (especially population samples) were extracted and genotyped but later combined since they were from the same unhabituated individuals. Any sample that had the same microsatellite genotypes at all screened loci and that were assigned the same genetic sex, regardless of the group or sex assigned tentatively in the field, were considered to be multiple samples of the same individual. Samples that had mismatches at up to two loci were re-examined for possible genotyping errors, allelic dropout and whenever possible, additional samples (at least 2 more independent samples that were independently identified and assigned as that individual in the field) were independently extracted and genotyped to confirm identity.

Five individuals (3%) from those collected that were run through the extraction protocol did not yield quantifiable DNA for subsequent genotyping, a result of having only one to two poor quality samples from individuals in the beginning of the study that had subsequently disappeared (n=2) or unhabituated individuals targeted during population censuses (n=3). The final sample set included 102 individuals from the 4 focal groups and 39 individuals in the census population (Table 3.1). Both adult males (n=20) and females (n=76) were represented in the analysis in addition to non-adult males (n=21) and females (n=24) (Table 3.1).

Genotyping across the panel of 19 microsatellite loci targeted in this study were 86% complete with a mean of 8.63 alleles per locus and expected heterozygosity of 0.78 (Table 3.2). Individuals (n = 141) were scored using at least 15 loci and four additional loci (D1s1665, D2s442, D4s2408 and Fesps) were optimized towards the end of the laboratory period. Thus, habituated individuals were typically genotyped at up to 19 loci to further confirm paternity results, while individuals where only one sample was available were often not genotyped at all loci due to the quantity of template needed to complete replicates across this large a panel of loci. Null alleles were not detected across the suite of loci for this population. Tests for linkage disequilibrium did indicate linkage at some combinations of loci, although rarefaction analysis indicated that pairwise genetic relationships can be confidently assigned with a total of 8 loci from the panel and values did not vary significantly with the exclusion of the linked loci. Given population allele frequencies based on all (adult) individuals sampled, the probability that any 2 individuals drawn at random from the population would share the same multilocus genotype by chance, i.e., the total probability of identity, $P_{(ID)}$ (Paetkau and Strobeck 1994) was 4.06×10^{-22}, and the chance probability of identity among full siblings, $P_{(ID)SIB}$ (Evett and Weir 1988), was 1.00×10^{-8} (Table 3.2, Figure 3.2). With the extremely low probabilities that any two individuals share the same multilocus genotype by chance, especially among the more conservative measure among full siblings, the results indicate that the panel of loci can reliably discriminate between related individuals within this sample set.

Genetic variation

A summary of the variation in the 19 microsatellite loci typed for all 141 individual Phayre's leaf monkeys sampled is presented in Table 3.2. Allelic diversity ranged from 5 to 14 alleles per locus (mean = 8.6). For most loci (14 of 19), observed heterozygosities were slightly higher than expected (paired t-test: $t_{18} = 3.218$, $P = 0.005$). Expected heterozygosities (H_e) across loci ranged from 0.66 to 0.88 (mean = 0.78), whereas observed heterozygosities (H_o) ranged from 0.58 to 0.95 (mean = 0.83). Further details of allele frequencies for only adult individuals (n=98) sampled are included in Table 3.3a (see also Chapter 2), where all adults were treated in the analysis as coming from one population. Allelic diversity again ranged from 5 to 14 alleles per locus (mean = 8.9) and observed heterozygosity (Ho = 0.85) was higher than expected (He = 0.79). Results also indicated significant deviations from Hardy-Weinberg equilibrium (HWE) expectations at 5 of the loci (Table 3.3a). Thus, further analyses were conducted with the population treated as distinct groups (PA, PB, PS, PO and Census individuals; Tables 3.3b-f). At the group level, three of the five groups still had over one marker in violation of HWE, but no one locus was in violation across more than one focal group (Tables 3.3b-e). Such mild deviations from HWE are expected given the likely presence of related individuals in the sample (Bourgain et al. 2004, Lukas et al. 2005, Bergl and Vigilant 2007) and given the number of different tests conducted (e.g., if testing 20 loci, it would be expected (by chance alone) that one would be out of HWE if the alpha level is set at 0.05.

Maternity and Paternity Exclusion

The suite of polymorphic loci is suitable for parentage analysis with a total exclusionary power generated from allele frequencies of >0.999 for the first parent (i.e., neither parent known), 1.00 for the second parent (one parent known) and a combined non-exclusion probability including a parent pair of 3.10 x 10^{-13} (Table 3.2). Maternity was assigned at the 95% confidence level to 46 of the 64 offspring (72%) in this study. The unassigned maternities are most likely due to the fact that not all candidate mothers were included due to the limited sample subset.

Natal individuals were assigned a mother with strict confidence in 39 of 41 cases (95%). All natal individuals whose mother's was assigned with confidence matched behavioral observations of mothers assigned in the field. The two unassigned natal individuals included one female (A7.1) and one male (Am4.1) from the PA group. A7.1 was a dependent offspring at the start of the study whose mother disappeared early in the study just after weaning A7.1 and prior to fecal sample collection. A7.1 is the only natal female observed to stay to reproduce successfully in her natal group (A7.1). While it is uncertain what happened to the mother (A7), the results confirm that she was not sampled in any of the census groups. In addition, we found one case in which an offspring was incorrectly assigned to a female as a mother-offspring pair (A4-Am4.1) through behavioral observation alone. This was surprising because, although it was early in the study when Am4.1's tentative mother overlapped in the group, the dyad was in close association and no other suspected maternal candidate was suspected through observation or confirmed through genetic analysis. I am positive that both A4 and Am4.1 were sampled correctly since the few samples from A4 matched with her later offspring (A4.2) and multiple samples were run over the span of several years for Am4.1 all deriving the same genotypic profile. Rather, it is possible, that a lag in systematic behavioral observation at the beginning of the study might have resulted in a missed event of either a female leaving her infant in the group or other more unlikely scenarios in which the mother died or come into a group with the infant and subsequently left. It is unlikely that the young male entered the group from another alone or in an all male band given his young age and fact that he is the only young male within his cohort in question. Most likely, this mismatch in observed and genetic maternity due to the close affiliation with the presumed mother (A4) may be a case of adoption.

Of the 8 females (young adult and immature) in the PO group whose origin was uncertain at the start of habituation and fecal collection, 50% were assigned to mothers from the candidate pool at the 95% confidence level. Results indicate that two of these females (OPOP10 and OPOP13) were natal to the group in which they were sampled from (PO) with assigned mothers sampled from the same group. OPOP11 was an adult female collected in 2006 prior to habituation of all individuals in PO that was assigned to a young female (O13) that only immigrated into PO in 2007. It is more likely that O13 was a daughter (O13) – mother (OPOP11) dyad or full sibling due to O13's young age (dyadic r = 0.72). Since OPOP11's entire history is unknown, she could have been temporarily visiting PO during sample collection and O13 later emigrated into the same group when OPOP11 was no longer there (for more details see Chapter 4). The additional female (O12) did not have a mother in PO but was assigned to a census female (POP29) sampled from an unhabituated group at least three territories (based on known group ranges) over to the southwest. The additional four uncertain females did not have any most likely mothers assigned.

Of the 15 females that immigrated into focal groups, only 3 had mothers strictly assigned, another 3 had a female assigned under relaxed confidence limits, and 9 females did not show evidence of mothers in the candidate maternal pool. From those strictly assigned, it appears that one female (A14) transferred from the PO group in relatively close proximity to PA (two home ranges over, although the groups occasionally had encounters). The additional two assignments were from the dyad A18 and S6, who were both young immigrant females, but more likely results from full-sibling relationships due to the young age of both females. One (S1-S9) of the three mother-daughter dyads assigned with relaxed confidence potentially provides support for a natal female leaving and returning to her natal group after several years; however, it should be noted that her assigned mother was no longer present when S9 temporarily joined PS (for further details see Chapter 4). In addition, since S1 was not assigned strictly to S9 and mismatched at one allele, it is also possible that this relationship is rather as siblings (dyadic r = 0.28). The two other females with mothers assigned within relaxed confidence limits appear to be from groups (or at least have relatives residing in these groups) several home ranges over from the one they were observed to immigrate into. Mothers could not be reliably assigned to the additional 9 females. It is possible that the mother may have been missed due to the fact that many of the individuals (e.g., females) within the neighboring groups were, in fact, not sampled during censuses. Alternatively, this could indicate a larger dispersal distance of some females outside the area sampled. Nonetheless, no mother-daughter or mother-son pairs resided in groups long-term.

Maximum likelihood analysis for paternity with mothers unknown resulted in 45 of 64 (70%) assignments of most likely fathers at the 95% confidence level. Natal individuals were assigned a father with strict confidence in 38 of 41 cases (93%) and a resident group male was assigned as the most likely father for 35 of the 41 natal offspring (85% of the time).

In one-male groups (PB and PS), most infants, were sired by the resident male. In PB, 82% of the offspring for which fathers were strictly assigned were sired by M5. However, three natal males (Bm2.1, Bm9.1 and Bm12.1) from the oldest cohort in PB had the same father (M9) strictly assigned from the neighboring group. For the two additional males from this cohort, Bm10.1 had the resident male (M5) strictly assigned as his father, while Bm6.1 did not have a father assigned with confidence (see below). Paternity results for father-son pairs assigned with confidence provide support for one or more of three potential scenarios, including: (1) extra-group conceptions/paternities, (2) females transferring from the PO group to join the neighboring PB group either pregnant or with dependent offspring, or (3) females transferring with their offspring and one of the resident males after the PO group fissioned. Six of the seven natal offspring for the PS group were sired by the resident male (M4), with one offspring not assigned (see below). Within the multi-male group PA, it appears that reproductive access to females is shared among the two adult males across years (age cohorts) and even individual females (with maternal offspring between successive years often, but not always (i.e., A3), alternating between adult males). Of the 13 offspring with strictly assigned fathers, M3 (the younger male) sired over 60% (8 of 13 offspring) while M1 (the older male) sired slightly less (5 of 13 or 38%). M1 appears to have sired more in the earlier cohorts (while

M3 was still subadult) than later cohorts, most likely a result of male rank changes (Koenig and Borries 2012, Koenig et al. unpublished). Unfortunately, there were only 2 natal offspring sampled for the PO group, which consisted of up to 4-6 candidate fathers in the group at any time, but paternity results suggest that only one male, M9, had the majority if not sole reproductive access to females. This is further supported by the additional three offspring sired by M9 from the PB group. However, there is one example (see immigrants below) in which paternity suggests an additional male from PO (M10) also sired offspring. Three natal individuals (A7.1, Bm6.1 and Sm3.1) did not have a most likely father assigned. As discussed above, A7.1 was a natal female whose mother and, most likely, father had left the group when she was a young juvenile. This natal female is the only one documented to remain in the group to breed, which is likely due to the disappearances of her father and mother (for more details see Chapter 4). Bm6.1 was among a cohort of older unweaned infants in PB when habituation began and the sole resident male was not his father, nor the father of the majority of his same-aged group cohort (see above). Bm6.1's mother (B6) was potentially involved in an extra-group copulation; however, it seems more likely that the PB group was either newly established or fissioned from a neighboring group (PO), although none of the adult candidate males in PO were found as a likely father. The third offspring, Sm3.1, was from the smallest group PO for which the adult male (M4) was the sole reproductive male. It is possible that the mother (S3) had an extra-group copulation with another male, since his most likely father under relaxed confidence was from an adult male neighboring south of the PS group (POP50). While the male was not assigned as the most likely father, they still had relatively high dyadic relatedness (r=0.27). Alternatively, S3 could have come into the group pregnant or joined later with her dependent offspring. However, since the group was followed since 2002 and under consistent observation from March 2003 where both the resident male (M4) and mother (S3) were present, it seems that the birth of Sm3.1 in June 2003 was an extra-group conception.

Overall, it appears that males in one-male groups may not have as much reproductive control over females because while they sired the majority of offspring, there are some cases of offspring sired by males outside the group. Multi-male groups appear to have more exclusive control over group females but share this reproductive access to group females, although it appears that one male tends to sire most (if not all) offspring per cohort and this can span several years in a row that can result in related paternal cohorts among group offspring.

Of the 8 young females in the PO group whose status was uncertain, 4 females (50%) had fathers strictly assigned from the candidate pool. Two of these females (OPOP12 and OPOP13) had a resident group male (M9) assigned as the most likely father. While OPOP13’s mother was also assigned from the PO group, OPOP12’s was not. It is likely that both of these young females were, however, natal and OPOP12’s mother had secondarily dispersed prior to more complete fecal sample collection. The third female, OPOP10, whose mother was from the PO group, was not sired by any of the 5 resident males, but rather by a male (M5) in the neighboring group PB. This could indicate an extra-group conception by her mother (O8) or evidence that the groups had fissioned prior to habituation with OPOP10 remaining in the PO group with her mother after her father left to either establish a new group before eventually emigrating herself. The most likely sire of the fourth female, O12, was a male from a group several home ranges over to the southwest. Since this group was the same in which a mother was confidently assigned for O12, there appears to be strong support that this was O12's natal group prior to immigrating into PO in 2007. Of the additional four females with unassigned paternities, OPOP11 did not have a father assigned and thus provides further support that she was temporarily in PO during a targeted sample collection early on in the study but not originally from the group (i.e., natal; see above under maternity).

From the 15 females that immigrated into focal groups, only 3 (20%) had fathers assigned with strict confidence. Two of the females show support of a relatively short female dispersal distance. Thus, results for both maternity (O1) and paternity (M10) support A14 as natal to group PO prior to immigrating into the PA group. Similarly, A22 was assigned to a father in a neighboring group just south of her new group PA. While A17 only had relaxed support for a maternal assignment (POP19), interestingly a father (POP20) was strictly assigned from the same group and likely indicates that A17 originated from several territories (over 5) southwest of the PA group.

Maximum likelihood analysis for paternity of the 39 natal offspring with mothers known through both observation and maternity analysis was also conducted. Of these natal offspring, 36 of the 39 (92%) had most likely fathers that were strictly confirmed and matched that of paternity results when mothers were presumed to be unknown. The 3 offspring (Sm3.1, Bm6.1, and Bm9.1) were all from one-male groups. Surprisingly, Bm9.1, who had been assigned to a neighboring group male (M9) in analysis with an unknown mother, no longer showed confidence in assigning paternity after including his mother's (B9) genotype and actually selected two alternative males (POP2, $r = -0.027$ and M11, $r = -0.010$) as the most likely paternal candidates. Since Bm9.1 and M9 did not mismatch at any loci in the previous analysis and also displayed a high degree of dyadic relatedness (r = 0.39), there appears to be the most support for this father-son relationship, although we are also certain through behavioral and molecular data that B9 is his mother. Thus, this particular paternity assignment should remain inconclusive.

Genetic relatedness across and within groups

Pairwise dyadic relatedness was analyzed for all individuals in the population and then averaged across groups into categories for all males and females, adult males and females and non-adult males and females (Table 3.4, Figure 3.3). Same sexed individuals were not highly related in the population. The average relatedness for all females (R = -0.010 ± 0.002 SE) was slightly higher than that for all males (R = -0.025 ± 0.006 SE). For adult individuals overall, adult females were slightly more related (R = -0.013 ± 0.002 SE) than adult males (R = -0.053 ± 0.012 SE), although same-sexed dyads were present both within and between groups. As expected, average relatedness of both male (R = -0.050 ± 0.012 SE) and female (R = -0.048 ± 0.011 SE) non-adults was relatively similar. In the population overall, same sexed individuals of both sexes are not closely related.

Looking more closely within independent focal groups (Table 3.5, Figure 3.4 and 3.5) gives a better indication of group dynamics and membership on mean group relatedness values. Here, groups were treated independently in analysis in relation the background of allele frequencies for the whole population and then averaged across groups. When considering specific groups, the average relatedness of all individuals (R = -0.041 ± 0.017 SD, range -0.067 to -0.026) and adult individuals (R = -0.065 ± 0.038 SD, range -0.127 to -0.026) was still rather low. The smallest group (PS) had the fewest relatives in the group overall (R = -0.067). Again, I found that adult females had slightly higher average relatedness (R=-0.055 ± 0.031 SD, range -0.100 to -0.030) than adult males (R = -0.119 ± 0.214 SD, range -0.365 to -0.017). However, it should be noted that in two groups (PB and PS) there was only one adult male and thus average male relatedness could not be calculated. In addition, males had a greater range in within group relatedness. The two adult males in PA were the least related (r = -0.365) and the 5 adult males in PO still had a low average relatedness (R = -0.017) while the census males had slightly higher average relatedness (R = 0.025) overall. Generally, in two (PO, census) of the three groups with multiple males, adult males were slightly more closely related than females. For adult females, again the smallest group (PS) had the lowest mean relatedness (R = -0.100) and females in PB (the largest group) had the highest average adult female relatedness (R = -0.029). Mean relatedness for adult male-female dyads was low overall (R = -0.124 ± 0.082 SD). Non-adult individuals from the four primary focal groups had a higher average relatedness (R = 0.012 ± 0.018 SD) than adults, and non-adult females (R = 0.051 ± 0.042 SD) were slightly more related (R = 0.028 ± 0.019 SD) than non-adult males (Table 3.5, Figure 3.5). Overall, the mean relatedness of non-adult male-female dyads was low (R = -0.007 ± 0.039 SD).

All focal groups contained related and unrelated adult female dyads and only one of the two focal groups with multiple adult males contained related male-male dyads. For PA, the two adult males were distantly related, while males were related in 3 of the 10 possible dyadic relationships among PO adult males (30%). For dyadic relatedness among males within the entire population sampled, male kin were present in 21 of 190 adult male-adult male combinations (11%) with related dyads with $r \geq 0.25$ in 6 cases and

15 adult male dyads with dyadic $r \geq 0.125$ to $r < 0.25$. Male relatives were present between focal groups (PA-PS, PA-PO, and PO-PB) and at least one male per group, excluding PA, had male relatives in the unhabituated male population censused. While there appears to be a network of male relatives within the adult population sampled ($n=20$ males), none of the adult male kin dyads within or between groups appear to be father-offspring relationships (through paternity).

All focal groups also contained related and unrelated adult female dyads. Adult females were related in 5 of the 28 possible dyadic relationships (18%) within PS (1 with $r \geq 0.25$, 4 at $r \geq 0.125$ to $r < 0.25$), 21 of the 120 possible dyadic relationships (18%) among PA adult females (6 with $r \geq 0.25$, 15 at $r \geq 0.125$ to $r < 0.25$), 14 of the 55 possible dyadic relationships (25%) within PO (6 with $r \geq 0.25$, 8 at $r \geq 0.125$ to $r < 0.25$), and 17 of the 105 possible dyadic relationships among PB adult females (16%) including 4 with $r \geq 0.25$ and 13 at $r \geq 0.125$ to $r < 0.25$ level relationships. Overall, adult female relatives were present in 402 of the 3003 potential dyadic combinations (13%) within the entire population sampled, including 96 related dyads with $r \geq 0.25$ and 306 related dyadic relationships at $r \geq 0.125$ to $r < 0.25$. Female relatives were present between all focal and census groups (Figure 3.6). Related female dyads were also present within the census population itself (Figure 3.7) and many adult females within each of the focal groups had female relatives in the unhabituated female population sampled during censuses (Figure 3.8). Again there appears to be an extensive network of female kin with the population of adult females included in this study ($n=78$). Within groups, however, there are no examples of mother-adult female offspring dyads. In addition, there is only one case (A14) in which a female from one of the focal groups (PA) has a mother in another focal group (O1 from PO) indicating a short dispersal distance and one other case in which a focal female O12 had both parents assigned from the census subset several territories over from the group in which she was currently residing (see maternity above). The other mother-female offspring dyads that had pair confidence in maternity assignments for an adult female (A18 and S6) was likely a full sibling relationship due to the young age of the two females assigned with confidence (both pre-breeding). All other adult immigrant females were not confidently assigned to a candidate mother, indicating the mothers were not included in the maternal subset sampled.

Population structure and sex-biased dispersal

Test results for sex-biased dispersal (F-statistics) are included in Table 3.6. The inbreeding coefficient (F_{IS}) across sexes and age classes suggest a low overall level of inbreeding within the population, with values that did not differ significantly from zero. As expected, F_{IS} values for non-adults showed a slight reduction in heterozygosity (F_{IS} = -0.175) compared to that of adults (F_{IS} = -0.60). Average F_{IS} values of both adult males and females were relatively similar, indicating that there is a mix residents as well as immigrants coming from different social groups for both males and females. However, adult females had a slightly higher F_{IS} value compared to non-adult females compared to that of males (Figure 3.9). The results not only provide support for female dispersal in this population, but also indicate the movement of males in the dispersal landscape as well.

Results for Wright's fixation index (F_{ST}) show gene flow and genetic variation across groups in this subpopulation of *T. p. crepusculus* (Table 3.6, Figure 3.10).

Pairwise F_{ST} comparisons indicated little genetic differentiation between same-sexed adults and only moderate differentiation among same-sexed non-adults. There was a slightly higher degree of genetic differentiation for adult males ($F_{ST} = 0.029$) compared to adult females ($F_{ST} = 0.012$). In contrast, non-adult females showed the highest, although still moderate, genetic differentiation ($F_{ST} = 0.082$) compared to non-adult males ($F_{ST} = 0.049$) even with similar sample sizes.

Assignment indices were calculated for all adult and non-adult individuals of both sexes (Table 3.6). For both adults and non-adults, the mean corrected assignment index (mAIc) was similar, although the value for males was slightly positive while the mAlc for females was slightly negative (Figure 3.11a,b). Although the variance in the corrected assignment index (vAlc) for adult females was slightly greater than that for adult males, there is still no significant difference in assignment indices to indicate a bias in dispersal by either sex (Mann-Whitney Test: $U_{(20,78)} = 761$, $Z = -0.167$, $p = 0.867$). In addition, the overall frequency distribution of Assignment Indices for males and females were similar, suggesting little bias in dispersal among the sexes (Figure 3.12 a,b).

DISCUSSION

Genetic variation, population substructure and gene flow in both sexes

Sex-biased dispersal patterns can be inferred using a combination of genetic markers (Di Fiore 2009, Goudet et al. 2002, Lawson Handley and Perrin 2007). Microsatellite markers are widely used to give insight into dispersal patterns and both males and females carry this information for autosomal markers. Unlike mitochondrial or Y-chromosome markers, genetic structure in autosomal microsatellite markers is not expected in populations in which both sexes disperse since both males and females disperse this material (Avise 1994). Thus, if both males and females disperse, autosomal markers should show little to no structure since individuals would transfer between groups mediating geneflow (Avise 1995), although one sex usually disperses over a longer distance. Alternatively, a pattern of high structure across all markers could suggest low levels of dispersal by both sexes if individuals are non-randomly selecting if and where to disperse, perhaps due to high costs of dispersal or anthropogenic factors such as habitat modification (Goossens et al. 2006). In examining loci characteristics across the population and within groups, I found evidence of genetic substructuring within the population indicated by the fact that some loci deviated from Hardy-Weinberg expectations when pooled as one large population, although no one loci exhibited deviations from Hardy-Weinberg expectations across groups (considered as a breeding unit). Mild deviations from Hardy-Weinberg equilibrium can be expected given chance as well as the likely presence of related individuals in the sample (Bourgain et al. 2004, Lukas et al. 2005, Bergl and Vigilant 2007). This finding could also be consistent with the Wahlund effect, or a disequilbrium caused by treating several separate populations as one (Wahlund 1928) arising from the presence of population substructure (Goossens et al. 2006). However, while the dispersing sex should be less differentiated in its allelic frequencies, it appears that there is both male and female gene flow and little genetic structure within either of the sexes.

The level of inbreeding across sexes and age classes did not indicate non-random mating or concern for inbreeding and this population appears to be genetically healthy despite relative isolation from other populations. As would be expected, non-adults showed a slight reduction in heterozygosity compared to that of adults and average F_{IS} values of both adult males and females were relatively similar. Genetic variation showed slightly more structure in males compared to females, as would be expected for the more philopatric sex, but this was not significant between the sexes. Overall, tests for sex-biased dispersal and the overall low average relatedness between both sexes did not indicate any genetic bias in dispersal by either females or males in this population.

Similar to what has been described for other folivorous primates (Moore 1984), female dispersal in Phayre's leaf monkeys is quite common (Borries et al. 2008, Chapter 4) and male dispersal has been documented as well but the extent remained unclear (Koenig and Borries 2012). However, contrary to what has been described from primarily observational studies in other female dispersal species (red colobus, Marsh 1979; hamadryas baboons, Moore 1984; gorillas, Stokes et al. 2003, Bradley et al. 2007) and colobines (Thomas' langurs, Steenbeek 1999, Sterck 1997, 1998), genetic evidence suggests that there does not appear to be a female bias in dispersal. Rather both sexes are dispersing genes to an appreciable degree. In fact, other Asian colobines have been described as having frequent male dispersal (review in Kirkpatrick 2011) and studies incorporating both molecular and behavioral evidence in female dispersal species have similarly found molecular support for gene flow by both sexes and low levels of overall relatedness between sexes (e.g., chimpanzees, Vigilant et al. 2001, Lukas et al. 2005; woolly monkeys and some spider monkeys, Di Fiore et al. 2009).

While further analysis of additional populations as well as sex-specific markers (Y-chromosome and mitochondrial) might shed further light onto the dispersal structure (e.g. Inoue et al. 2013), it appears that both males and females are dispersing genes within this population to varying degrees. These results are consistent with the fact that demographic observations indicate frequent female dispersal and males often remain in their natal groups or territories (after forming new groups) or disappear with uncertainty (death or dispersal of longer distances). While genetic evidence indicates similar dispersal by both males and female, coupling observational data provides a further understanding of how the partitioning of genes in this population are still mainly by females and males within natal groups or territories. Females mediate the extent of female as well as male gene flow due to both natal and secondary dispersal (Chapter 4) and the fact that females may transfer pregnant or with offspring and often reproduce in groups after secondarily dispersing. This can result in same-sexed kin within and between groups (see further discussion below). To a lesser extent, males also mediate gene flow by monopolizing reproduction over successive years (approximately 4 years) resulting in paternally related cohorts and also fissioning or more often dispersing and forming new groups with both related and unrelated offspring (see discussion below).

Male and female relatedness within and between groups

Dispersal and reproductive behavior influence the partitioning of genetic variation within and between social groups in a population (Altmann et al. 1996, Clobert et al. 2001, Di Fiore 2009). However, dispersal events are relatively rare and require longitudinal studies that may still result in missed events (Pusey and Packer 1987). Genetic structure of social groups can be described to some degree by purely molecular evidence of patterns of sex-biased dispersal (e.g., Altmann et al. 1996, Di Fiore and Fletcher 2005, Hammond et al. 2006). Tests for sex-biased dispersal typically work under the assumption that adults of the more philopatric sex will have higher mean levels of relatedness within groups and the dispersing sex will have higher relatedness among groups. However, combining both observational and genetic data can occasionally lead to seemingly contradictory results (Vigilant et al. 2001, Lukas et al. 2005, Goossens et al. 2006, Lawson Handley and Perrin 2007, Bradley et al. 2007, Harris et al. 2009, Inoue et al. 2013). Long-term studies of chimpanzees (*Pan troglodytes*) show that males are philopatric and females disperse, but genetic studies have found that average within-group relatedness usually does not differ between adult males and adult females (Vigilant et al. 2001, Lukas et al. 2005). Within-group relatedness for the philopatric sex may not be significantly higher than for the dispersing sex if group size is large (Lukas et al. 2005). In addition, low levels of average within group relatedness could result from non-random dispersal or if unrelated males reside in the group and multiple males sire offspring (Altmann et al. 1996).

From long-term behavioral and demographic observations in this population of Phayre's leaf monkeys, frequent female emigrations and immigrations have been well documented (Chapter 4), while new males rarely if ever (with one exception) immigrate into an existing group comprised of adult males, although males have left groups to form new groups or have disappeared with uncertainty. Longitudinal studies have shown that males may leave groups alone or in groups (Koenig and Borries 2012), which may include kin or non-kin. Thus, we expected males to be more related than females within groups and females to be more related than males between groups. However, in addition to low reproductive skew and shared or limited reproductive tenures monopolizing all females in a group, extra-group paternities as well as females secondarily dispersing pregnant or with offspring can decrease male genetic variation between groups (Schubert et al. 2011).

Both sexes showed low levels of average within group relatedness, which could result if unrelated males reside in the group and multiple males sire offspring (Altmann et al. 1996) or if males typically disperse from groups after reproductive tenure. However, due to the presence of both one and multi-male groups, this is likely not the only explanation (see below). This population of Phayre's leaf monkeys consists of both one and multi-male groups. Similar to what has been reported in Hanuman langurs (Borries 2000), one male groups appear to sire most offspring but tenure appears to be approximately short (ca. 4-6 years) and males in multi-male groups can have longer-termed access to females although, as described in Hanuman langurs (Borries 2000), they must share this access to some extent with other groups males (whether kin or not). Results indicate that male reproductive skew is not so pronounced in the adult communities; but, as expected, there are cohorts of similarly aged individuals within social groups for individuals prior to the age of dispersal and sexual maturity. In addition, there appear to be some infants for whom the father was not in the group during behavioral observations and sampling. These infants were likely sired by non-group males, and either is an indication of extra-group copulations, that the adult male was no longer in the group when sampling started (for young at the start of group habituation), a result of group fissioning, or female transfer to new or established groups either pregnant or with dependent offspring. One example from PB shows that group dynamics of PB and it's neighboring PO might have indicated overlap of either males or females at some point since at least some of the infants result in paternity exclusion from a male from the neighboring troop.

While frequent dispersal often leads to lower average relatedness in the dispersing sex, non-random dispersal may result in kin associations through immigration into the same group as kin. Thus, given the increasing evidence that same-sexed kin can reside in groups despite dispersal (Pope 1992, Bradley et al. 2007), it is not surprising that I found both related males and females within the groups. Non-random dispersal, usually involving cohort dispersal, has been described for both males in female philopatric primate species (e.g., Cheney and Seyfarth 1983, Jack and Fedigan 2004, van Noordwijk and van Schaik 2001; but see Chancellor et al. 2012) and in female dispersing species (Starin 1994, Watts 1994, Bradley et al. 2007, Chapter 4). Individuals may also disperse into groups consisting of related natal females or sequentially into groups in which related females already reside (Starin 1994, Di Fiore 2009, Chapter 4). In addition, despite initial dispersal, female kin groups can develop over time (Pope 2000) or additional social or anthropogenic factors that may lead to groups disbanding (Stokes et al. 2003, Di Fiore 2009), which could result in groups containing same-sexed relatives despite dispersal of that particular sex.

For Phayre’s leaf monkeys, however, it appears that female dispersal is an avenue for gene flow of both males and females. Females rarely remain philopatric (only one case in more than 23 group years) and thus, females may exhibit nonrandom dispersal and enter groups already containing female kin or disperse in kin cohorts. In addition, female secondary dispersal may result in same sexed kin present across groups if the mother secondarily disperses and reproduces in that group. From observations, there is evidence for males staying in their natal group in which kin groups could potentially develop, but this may be mitigated by the disappearance or dispersal (forming new groups usually within their natal range) of related males. However, male-mediated gene flow is also likely due to female secondary dispersal (pregnant or with male offspring) as well as occasional extra group copulations similar to what has been reported in patrilocal chimpanzees (Schubert et al. 2011). However, the fact that same-sexed adult dyads within groups were never close relatives (e.g., parent offspring or full sibling), could indicate greater dispersal distances for both females as well as potentially males that disappear, as recently described for western lowland gorillas (Inoue et al. 2013).

Male kin networks

Overall, adult males were not more closely related to one another than are adult females. While adult males showed some evidence of being more closely related than adult females within 2 of the 3 groups that contained multiple males, males still had a similarly low percentage (11%) of same-sexed kin within the greater population as females (13%). Furthermore, while males in both single and multiple male social groups were usually related to one or more nearby males, these were rarely, if ever, close kin (e.g., father-son dyads or full siblings). This may, however, be a result of our sampling bias because observational data has since shown an adult male (M4) dispersing with two sons in addition to an unrelated male juvenile from the group. However, we are uncertain if the related males remained together despite evidence that some related males left a group together. Closer examination of group differences also indicates that there might be greater variability of male within group relatedness. The low levels of male relatedness within groups could be due to the small sample size and result from a bias from one of the multi-male social groups. In two groups (PB and PS) there was only one adult male and thus average male relatedness could not be calculated. However, it should be noted that in both of these groups, natal males later matured in the group to reproductive status after the death of the adult male (PB) or the dispersal of the adult male (PS) included in the study.

Paternity results indicated that group males sire most offspring with reproductive tenure over the course of 4-9 years, although not all males that matured in a group were necessarily sired by the same adult male and thus close kin (e.g., Altmann et al. 1996, Bradley et al. 2005). Males in one-male groups seem to have rather long tenures and monopolize the group over at least 4-6 years. While males in one-male groups appear to have exclusive access to females, there is some indication that policing females may be more difficult as evidenced by extra-group paternities. Some support of this is from the PS group with Sm3.1. It is also possible that additional males had been present and sired offspring or groups were newly formed as a result of fissioning or male dispersal prior to the start of the study. This appears to be the case in PB, where intergroup interactions and the atypically small male to female ratio indicate this group may have fissioned from the neighboring group PO, and some of the pregnant females followed the PB male or alternativiely, one of the PO males left to form a new group and females either followed at that time or later, or additional females joined.

Males in multi-male groups appear to sire all group offspring for longer durations (up to 9 years), although, similar to what has been described in Hanuman langurs (Borries 2000), mountain gorillas (Bradley et al. 2005), and chimpanzees (Vigilant et al. 2001), males may share access to females resulting in mixed paternity of offspring either in a given cohort or across years, although the one male usually predominantly sires most offspring in line with male turnovers in rank. One male (M9) was the dominant sire to most offspring in the other multi-male group (PO), and it appears that other group males may have remained in the group waiting for reproductive opportunities since the dominant male rarely has full control over all females unlike in red howler monkeys (*Aloutta seniculus*, Pope 1990). Since some of the males in PO were kin, they could be indirectly increasing inclusive fitness by participating in territorial defense with the dominant male. Eventually, however, several of the subordinate PO group males dispersed to form a new group since the benefits outweighed the costs of waiting with little to no reproductive output as has been described in ursine colobus monkeys (*Colobus vellerosus*) where males often emigrate to improve their reproductive opportunities (Teichroeb et al. 2011). Further examination is underway to fully ascertain male dispersal decisions and long-term reproductive success in this species (Koenig et al., unpublished).

Nonetheless, multi-male groups had a greater range of within group relatedness. The two adult males in PA were the least related and the 5 adult males in PO still had a low average relatedness while the census males had slightly higher average relatedness overall. It is possible that this low within group relatedness of group males could be a result of multiple unrelated males siring offspring within the same group that later mature and stay in the group, as mentioned above. In addition, long-term observation also lends for some additional explanations for the low relatedness of males within groups. In two cases when males formed new groups females joined them – and some of these females had young infants (personal observations, Koenig and Borries 2012). In addition, females (e.g., PS) have been observed to disperse with dependent infants. Thus, females may be responsible for dispersing male genes between groups leading to lower levels of relatedness within groups compared to between groups than would be expected by exclusive male philopatry. In addition, the PS male disperse with two of his sons in addition to a non-kin juvenile male from the group, leaving his other son in the group.

Contrary to what has been found in chimpanzees (Lukas et al. 2005) there does not appear to be an influence on group size in that higher average relatedness among the philopatric sex is expected in very small groups. In fact, even with extensively documented male philopatry, researchers have not found a significantly higher average relatedness of philopatric chimpanzee males as compared to females within groups (Vigilant et al. 2001). The low levels of relatedness in Phayre's males may be a result of overall similar group sizes as well as the admixture of both one and multimale groups. As expected, the two one-male groups (PB and PS) had more non-adult kin within groups than the two multi-male groups (PA and PO) indicating that males might not monopolize total reproductive access to group females.

Male dispersal may vary among groups and time, with relatively long male tenure (e.g., M1 in PA) but potential turnover of reproductive monopolization (e.g., M1 and M3 in PA) with one male potentially siring most infants over the course of a few years (PA and PO) (for more details on male rank and membership changes see Koenig and Borries 2012). This pattern in males is similar to what has been described in chimpanzees (Vigilant et al. 2001, Lukas et al. 2005) as well as mountain gorillas (Bradley et al. 2005). The female dispersal strategy may also influence these male kin networks as females have been observed to display both natal and secondary dispersal and reproduce in multiple groups over a reproductive lifetime. Thus, male kin may be present in neighboring groups. In addition, the combination of multi-male groups (where one male doesn't sire all offspring) and female dispersal (where females in a particular group may not be related) could lead to males maturing in a group with unrelated but familiar males. Alternatively, or in addition, having unrelated adult males present in groups may also suggests that male immigration can sometimes occur despite few direct observations as seen in spider monkeys (Di Fiore 2009). In fact, we have observed males that have disappeared, left after over a year and returned briefly to leave again (Bm6.1) or alternatively left to form new groups. The low levels of male relatedness within and between groups indicated from dyadic relatedness and parentage analysis could support a large dispersal distance for some males that are unable to establish new groups in nearby territories similar to what has been reported in a population of western lowland gorillas (Inoue et al. 2013). While some unconfirmed male disappearances remain uncertain in this population, both adult and juvenile males have been observed to voluntarily leave groups in their reproductive prime as well as after male intra-group aggression (Koenig and Borries 2012). It is also possible that males may not leave groups, but groups disband or females within groups are more distantly related resulting in the maturation of several unrelated males in the group. From observations, it appears that males may mature in a group, but this often does not develop into residence of father-son pairs (excluding M1 and Am5.1 in PA from later in the study) or full sibling adult male dyads, since the father, son or brother eventually leaves the group. For example, in the one male group PS, when the son came into sexual maturity, the resident adult male (M4) left the group.

The varying level of relatedness in males may help explain social behavior among same-sexed individuals. In female biased dispersal species, males are generally more affiliative with one another than females and cooperate with each other in territory defense and within- and between-group encounters (spider monkeys, Di Fiore and Campbell 2007; chimpanzees, Watts and Mitani 2001). In woolly monkeys, however, male-male cooperation is rare, although occasionally in intergroup interactions and adult males are tolerant, but not overly affiliative with one another (Strier 1990, Di Fiore and Campbell 2007). While Phayre's males tend to tolerate one another rather than affiliate to any large extent, males have been observed to cooperate with each other in both within and between group encounters. Multi-male groups have larger home ranges (Gibson and Koenig 2012), a potential benefit from joint territorial defense, although cooperating can come at a risk. In fact, high intensity of intra-group aggression among adult males has also been observed as a result of rank changes (Koenig and Borries 2012) and injuries in multimale groups are common and may be due to competition among males for residence in a group. In one of the multi-male groups with unrelated adult males, overt aggression between males occurred when the younger male tried to throw the older male out of the group (resulting in the loss of an eye). However, the males continued to reside together in addition to the maturing sons of both males, and both males continued to reproduce. How this group continued to develop over time is less certain. While other adult males (e.g., M4) may choose to disperse when a son is coming of reproductive age. It still remains to be seen if and how genetic relatedness among males correlates to social behavior and long-term reproductive success (Koenig et al., unpublished). Nonetheless, the existing networks of male kin may provide the potential for kin-biased behaviors between groups (Bradley et al. 2004).

Female kin networks

Overall, adult female kin dyads were present in 13% of the entire adult female population sampled. All focal groups contained related and unrelated adult female dyads and female kin were present between groups. Again, there appears to be a network of female kin with the population of adult females included in this study despite female dispersal, which has been previously reported for other female dispersal species (western gorillas, Bradley et al. 2007), although Phayre’s females do not appear to stay in or immigrate into groups with either sons or daughters (Chapter 4). Females potentially enter groups in same-sexed cohorts similar to what has been described in red colobus monkeys (Starin 1994). However, unlike what has been described in howler monkeys (Pope 1990), females do not appear to stay in groups and develop matrilineal cohorts over time. Nor is there evidence that female kin actively evict less related females from the group (Pope 1990, Morelli et al. 2009), although there is directed aggression towards emigrating females prior to some dispersal events. In fact, no mother-offspring dyads were found within groups and only one mother-daughter dyad was found in neighboring groups. In fact, the only female observed to remain in her natal group (A7.1) did not have a parent in the group sampled. While there was evidence of related female kin residing in neighboring groups, most female-female genetic relationships were not highly related and in only a handful of cases did a mother and/ or full sibling reside nearby.

In addition, non-adult females from multi-male groups did not appear to be closely related within particular social groups, likely indicating the adult females are not necessarily closely related within a group and/ or the males in multi-male groups may share reproductive access to females. Thus, while females may disperse either with females (whether or not these are kin) or to groups containing kin (as described above), it seems that this is often outside of a female's natal territory. While there is the possibility that a female may stay in a group if the opportunity is there (e.g., A7.1), this is only one case. It still remains to be seen through further molecular markers and increased sampling localities exactly how sexes may differ in dispersal distance.

Females have been observed to leave and enter groups with same-sexed kin and may disperse nonrandomly to groups already containing female kin. Females have also been observed to exhibit secondary dispersal and a female may leave group with or without offspring and go to another group to reproduce, so genetically similar same-sexed individuals may be present in a neighboring group. In addition, male turnovers or group disbanding may influence the clustering or dispersal of female kin within the landscape similar to what has been described in western lowland gorillas (Bradley et al. 2007) and the ursine colobus (Teichroeb et al. 2009). While we have not observed several adult females disperse together following group instability or turnover, there are a handful of cases in which certain females may have left due to rank changes in males (e.g., A11), following the dispersal of certain males (e.g., A7), or reproductive maturation of their sons (e.g., S1) (for further details see Chapter 4). However, additional intra-sexual social factors may also have been involved. In addition, similar to the situation for males, multi-male groups or extra-group conceptions may lead to fewer female relatives within non-adults and more related females within the greater female community. While the dispersal strategies of females is discussed in more detail elsewhere (Chapter 4, Koenig et al. unpublished), the results do indicate the potential for female kin cooperation despite female dispersal. In fact, female Phayre's leaf monkeys display prolific infant handling and complex and affiliative social relationships (Larney, unpublished), which have been typically attributed to the maintenance of social relationships and fitness benefits among closely related kin (Silk 2002). Some studies have documented female kin associations in certain species despite female dispersal (e.g., red colobus monkeys, Starin 1994; mountain gorillas, Watts 1994; potential for western lowland gorillas, Bradley et al. 2007). And while some studies have shown that paternal relatedness, as indicated by age similarity (Altmann 1979), also influences sociality within social groups (Widdig et al. 2001, Smith et al. 2003), other studies coupling extensive behavioral and genetic data do not show preferential recruitment of maternal (Mitani et al. 2002) or paternal (Langergraber et al. 2007) kin for social or cooperative activities. Overall new studies suggest that kin selection may not be the primary reason for animals to group together and group membership is not necessarily reflective of kin residing together (Lukas et al. 2005). If and how genetic relatedness among females may correlate with access to ecological resources, development and maintenance of social behaviors and long-term reproductive success remains to be seen (Chapter 4, Koenig et al., unpublished).

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Figure 3.1 Location of Phu Khieo Wildlife Sanctuary and Study Site (Mai Sot Yai) in northeastern Thailand [Map detail from RTSD (1986) Changwat Phetchabun. 2nd ed, [topographic map], Bangkok, 1:250,000, Sheet NE 47-16, Series 1501S]

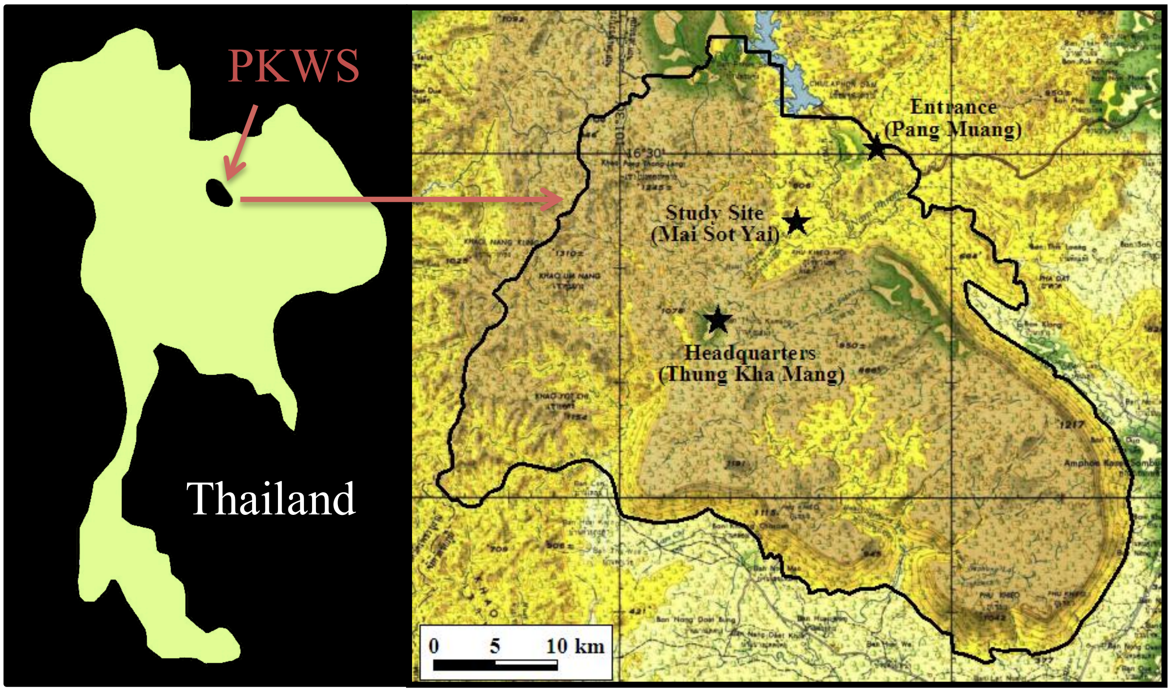

Figure 3.2 Relationship between the number of loci examined and the probability of both individual identity (P_{ID}) and sibling identity ($P_{ID\text{-}SIB}$). Statistical significance ($p<0.05$) was achieved after three or more loci (P_{ID}) or eight or more loci ($P_{ID\text{-}SIB}$) combinations

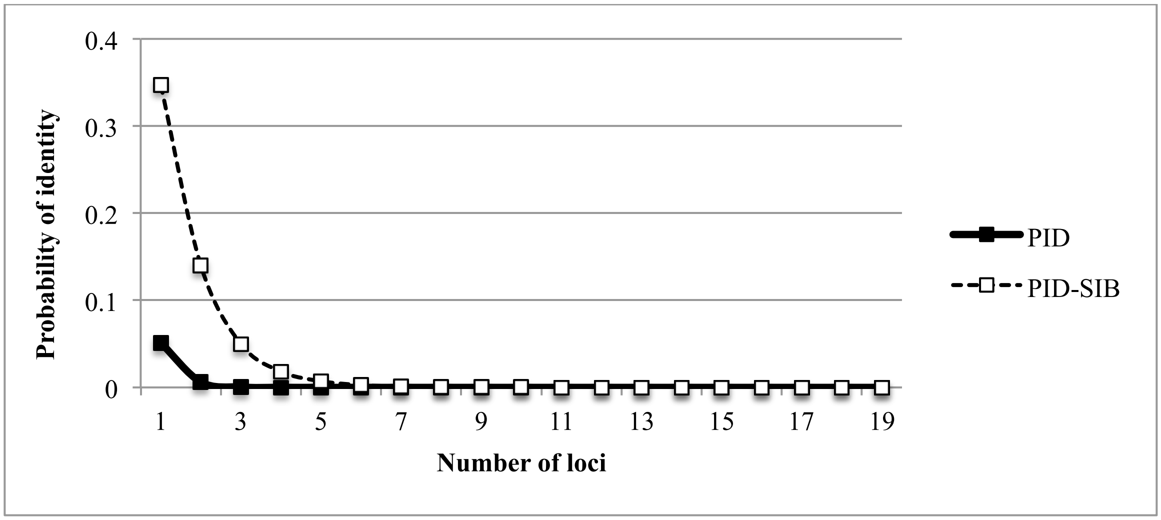

Figure 3.3 Observed average relatedness (± SE) among male (grey bars) and female (black bars) Phayre's leaf monkeys comparing adults versus non-adult individuals

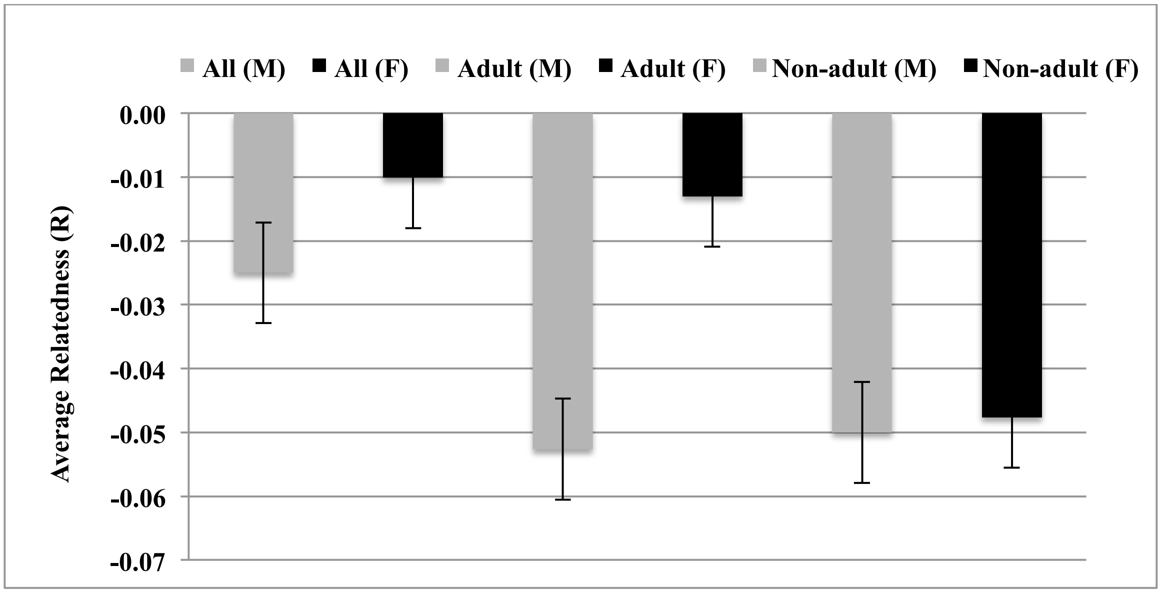

Figure 3.4 Observed average relatedness (± SD) among male and female Phayre's leaf monkeys comparing adults versus non-adult individuals across groups

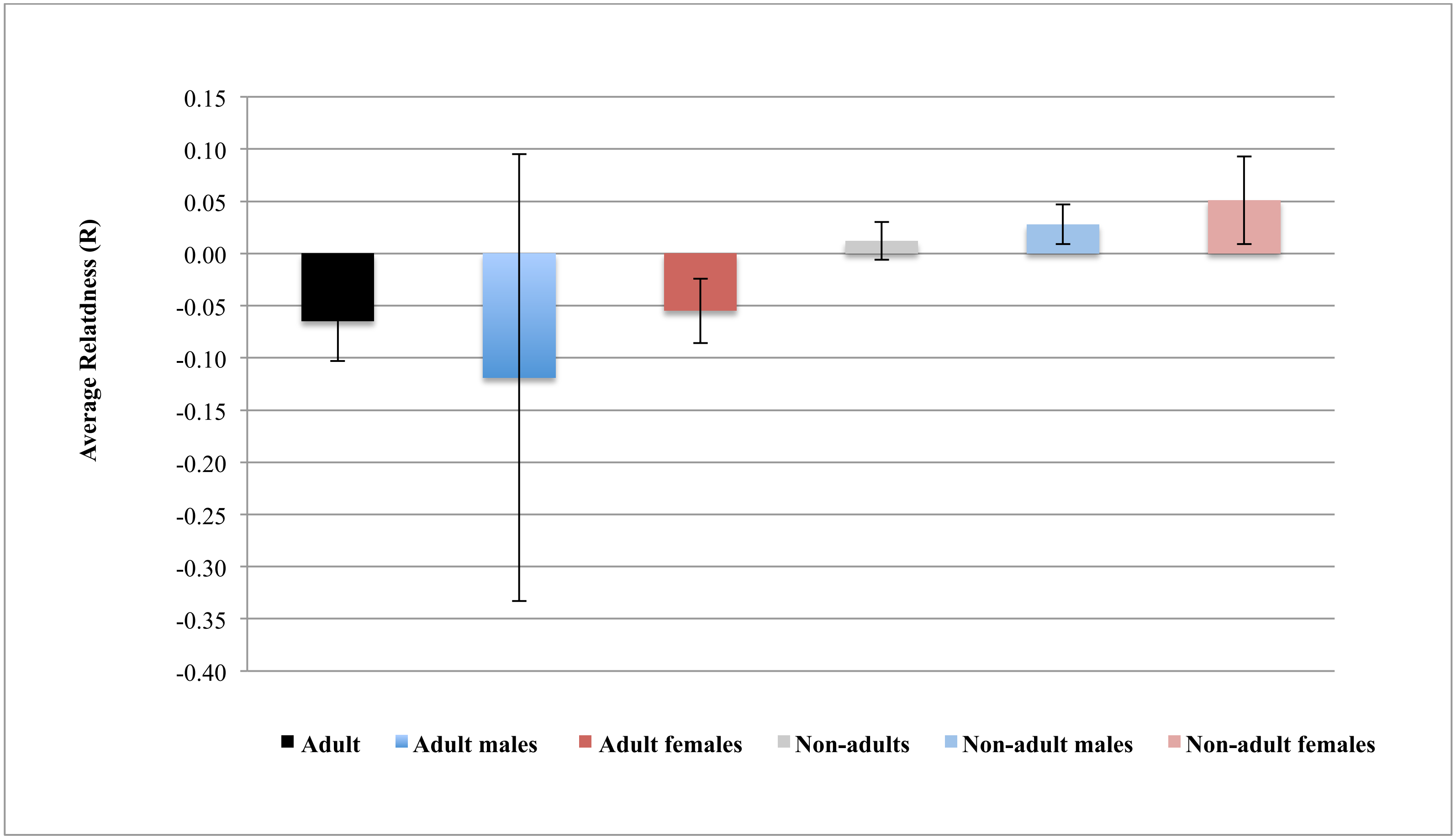

Figure 3.5 Observed average relatedness within focal groups of increasing size amongst adult and non-adult male and female Phayre's leaf monkeys

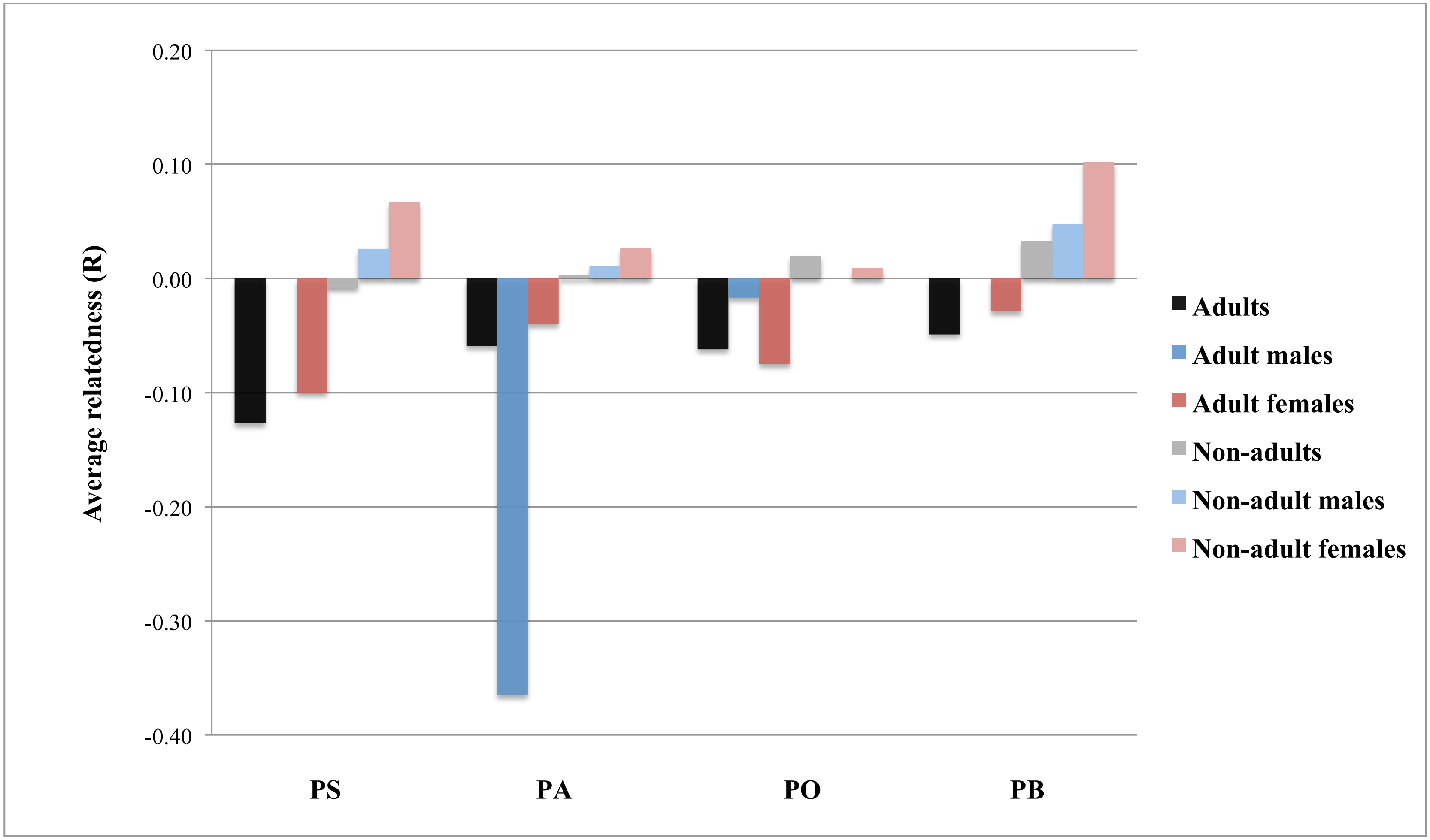

Figure 3.6 The cumulative sum of pairs of related dyads among adult females per focal group over the observation period. Focal groups are distinguished by color (PA – red, PB – green, PO – orange, PS – blue) and pairwise relatedness is indicated by solid (r ≥ 0.25) or dashed (r = 0.125 - <0.25) lines weighted by sum totals.

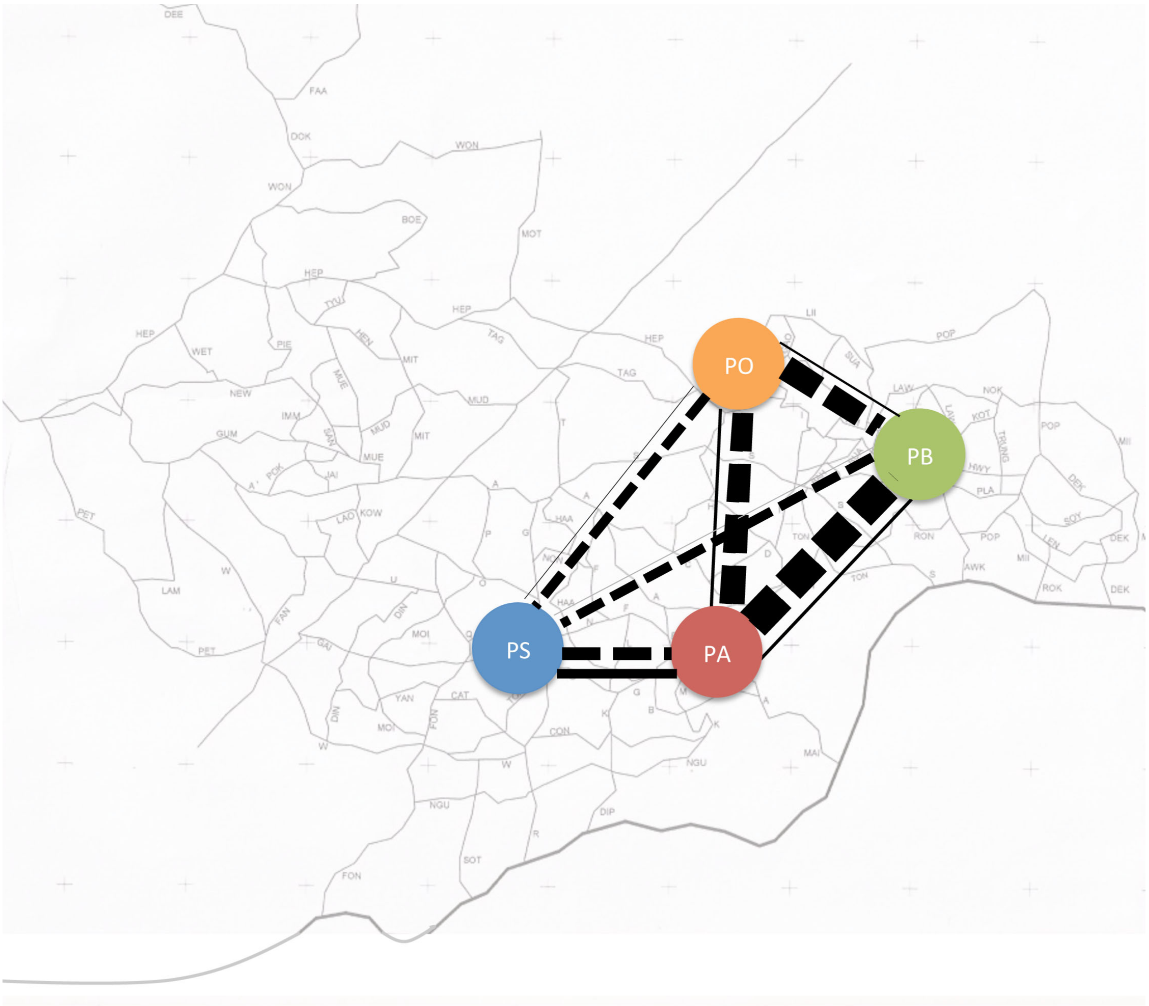

Figure 3.7 The cumulative sum of pairs of related dyads among adult females per census group location (tan) over the observation period. Pairwise relatedness is indicated by solid (r > 0.25) or dashed (r = 0.125 - <0.25) lines weighted by sum totals.

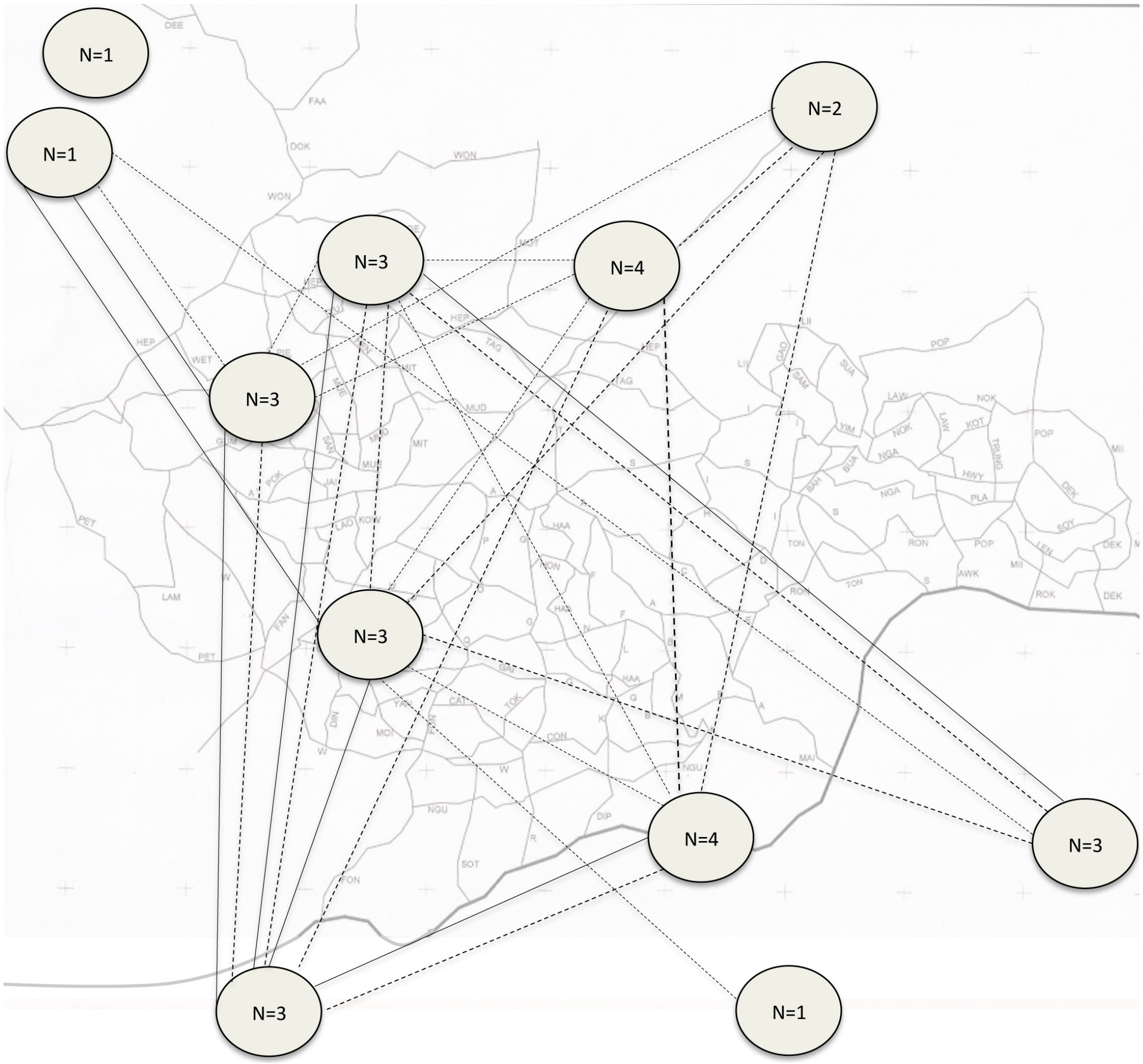

Figure 3.8 The cumulative sum of pairs of related dyads among adult females in census group location (tan) to focal group females (PA – red, PB – green, PO – orange, PS – blue) over the observation period. Pairwise relatedness is indicated by solid (r ≥ 0.25) or dashed (r = 0.125 - <0.25) lines weighted by sum totals.

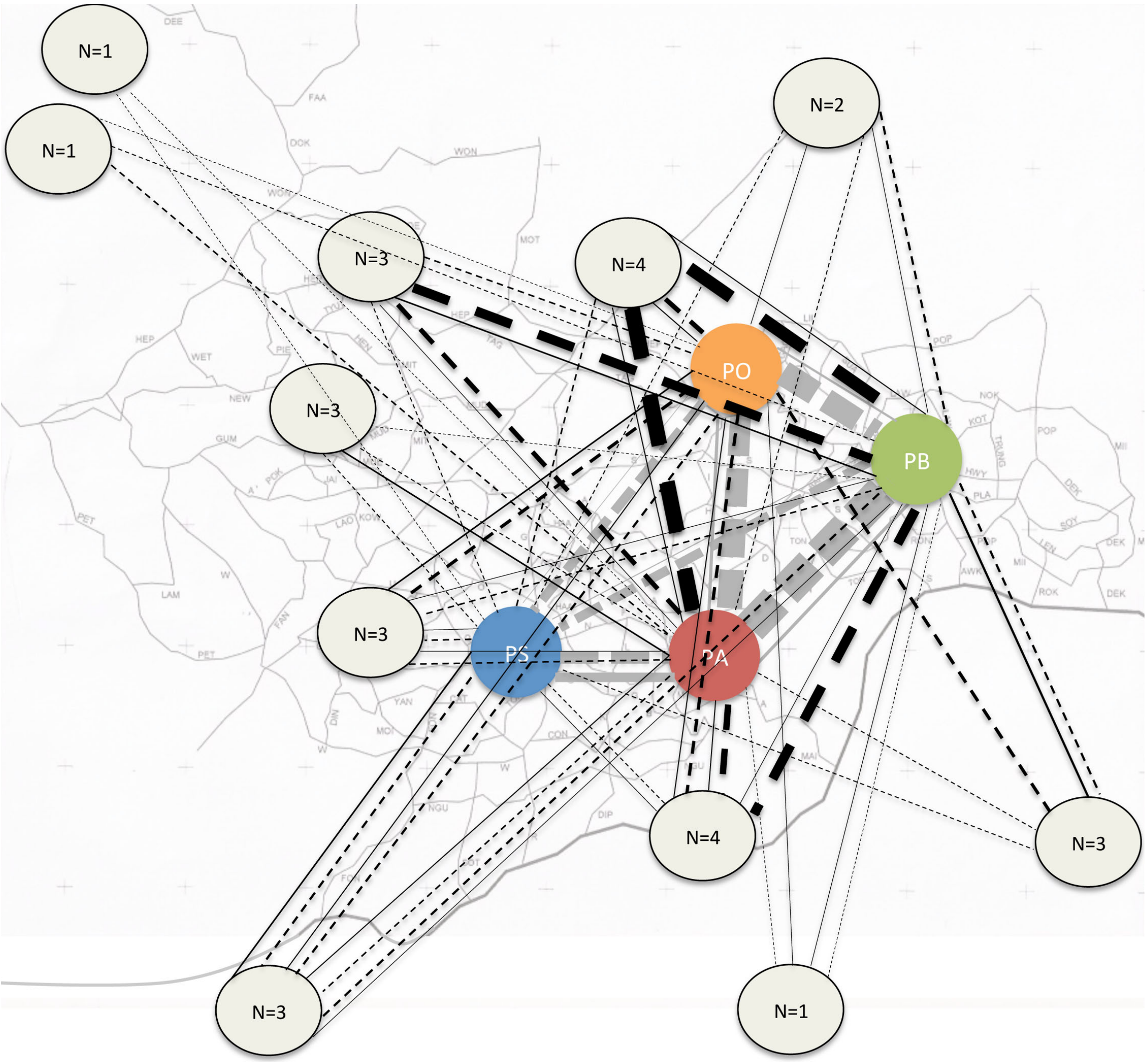

Figure 3.9 Inbreeding coefficient (F_{IS}) amongst adult and non-adult male and female Phayre's leaf monkeys

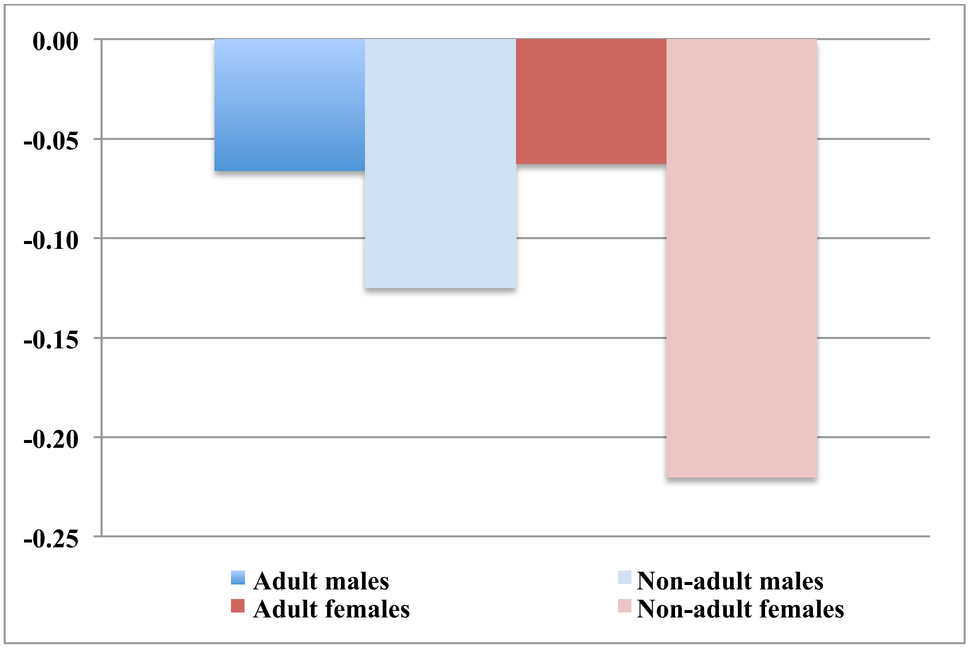

Figure 3.10 Genetic structure as indicated by Wright's Fixation Index (F_{ST}) for adult and non-adult male versus female Phayre's leaf monkeys

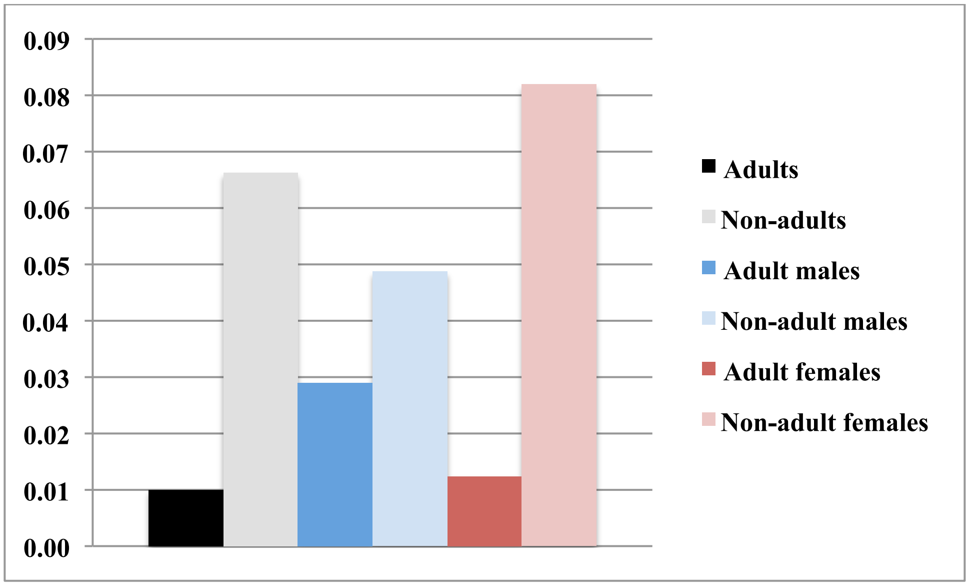

Figure 3.11a Overall frequency distributions of Assignment Indices in adult male and female Phayre's leaf monkeys

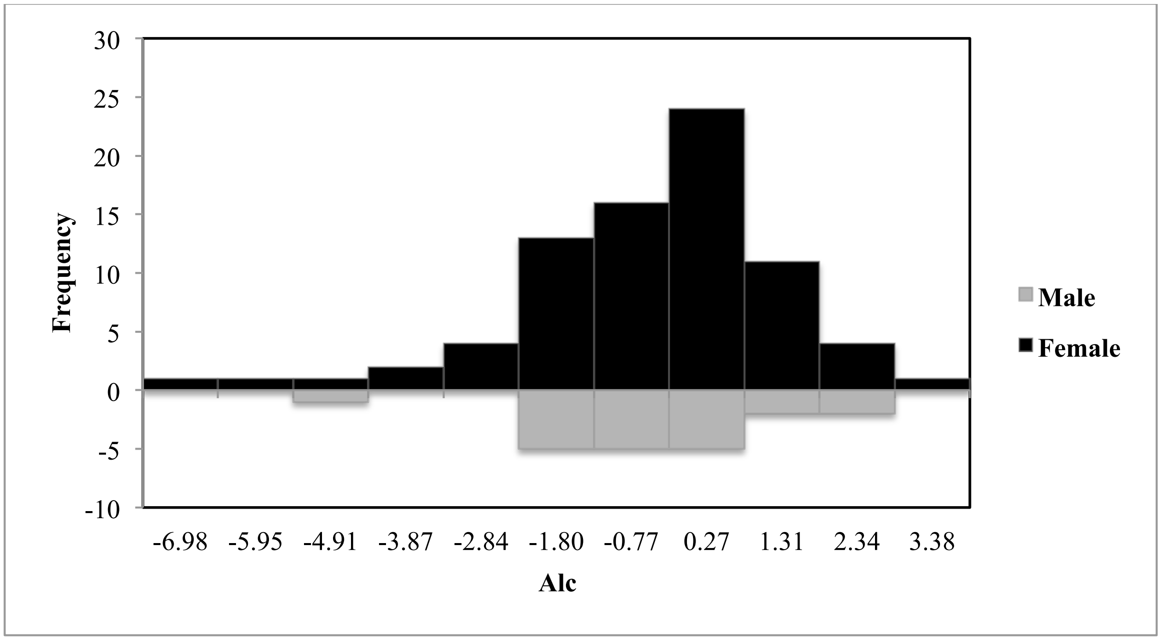

Figure 3.11b Overall frequency distribution of Assignment Indices in non-adult male and female Phayre's leaf monkeys

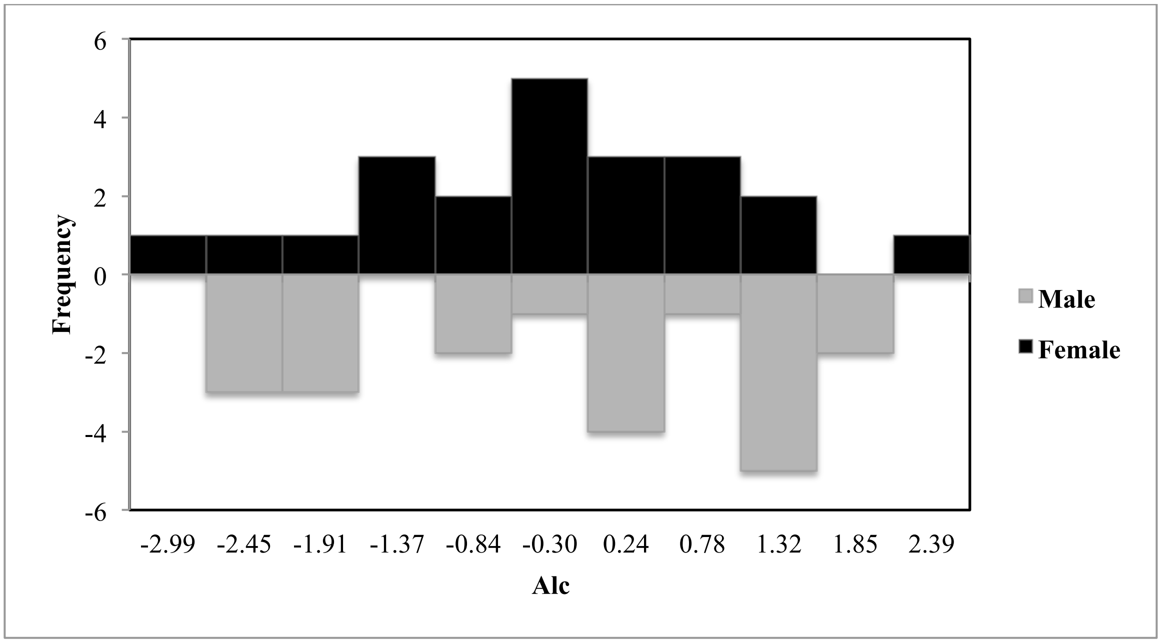

Figure 3.12a Average corrected Assignment Indices (mAIc ±SE) for males and females in adult Phayre's leaf monkey

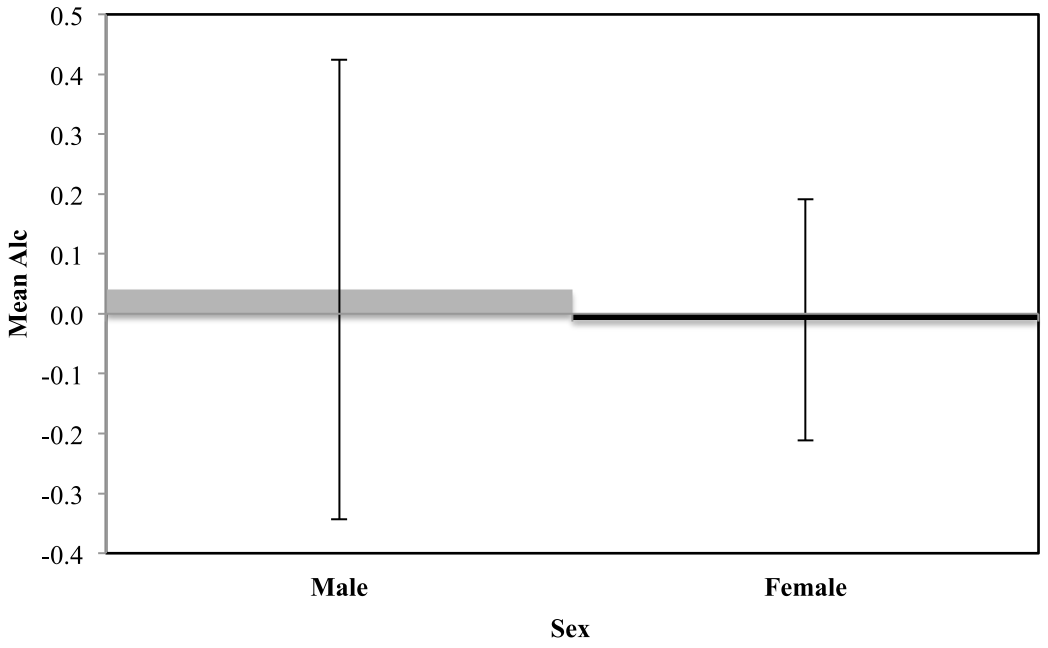

Figure 3.12b Average corrected Assignment Indices (mAIc ±SE) for males and females in non-adult Phayre's leaf monkeys

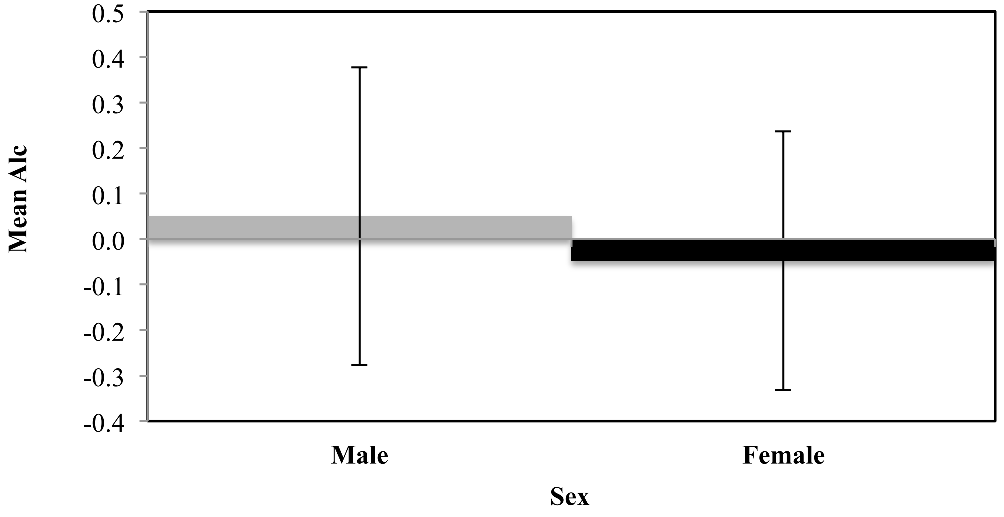

Table 3.1 Individuals and samples collected from Phayre's leaf monkeys in Phu Khieo Wildlife Sanctuary used in the molecular analyses

			Males		Females	
Group	No. Individuals	No. Samples	Adult	Non-adult	Adult	Non-adult
PA	31	95	2	5	16	8
PB	34	106	1	12	15	6
PS	18	53	1	3	8	4
PO	21	52	5	1	11	4
Census	39	78	11	^	28	^
Total	**141**	**384**	**20**	**21**	**78**	**22**

Notes:

(1) Individuals that dispersed into one or several groups are included in the primary/first group for analyses

(2) Overall, there was 97% success in extracting nuclear DNA from targeted individuals; however, 5 individuals sampled did not amplify during genotyping and were thus excluded from analysis

(3) ^ indicates that no non-adult samples were collected or used in genetic analysis for the census (general population) samples

Table 3.2 Summary statistics for the Phayre's leaf monkey population (n=141) genotyped at 19 loci

Locus	k	N	Ho	He	PIC	NE-1P	NE-2P	NE-PP	P_{ID}	$P_{ID\text{-}SIB}$	HW	F(Null)
D1s207	12	141	0.936	0.884	0.869	0.393	0.242	0.091	0.026	0.316	nd	-0.0305
D1s548	9	141	0.936	0.789	0.759	0.579	0.402	0.212	0.073	0.375	*	-0.0955
D2s1399	12	141	0.950	0.848	0.828	0.470	0.305	0.133	0.041	0.338	ns	-0.0626
D3s1766	9	141	0.879	0.865	0.846	0.442	0.281	0.119	0.035	0.328	nd	-0.0102
D5s1457	6	141	0.837	0.793	0.758	0.592	0.413	0.232	0.076	0.374	ns	-0.0279
D6s1280	6	141	0.844	0.807	0.775	0.570	0.392	0.214	0.068	0.365	ns	-0.0248
D7s1817	10	141	0.801	0.788	0.757	0.587	0.408	0.220	0.075	0.376	ns	-0.0118
D10s1432	12	141	0.752	0.704	0.675	0.682	0.495	0.285	0.115	0.428	ns	-0.0317
D11s2002	6	141	0.830	0.743	0.694	0.674	0.500	0.323	0.114	0.408	ns	-0.0584
D13s321	8	141	0.773	0.787	0.753	0.596	0.418	0.234	0.078	0.377	ns	0.0063
D14s306	6	141	0.865	0.754	0.708	0.659	0.482	0.304	0.105	0.400	*	-0.0741
D17s1290	14	141	0.837	0.834	0.812	0.494	0.325	0.147	0.047	0.346	ns	-0.0071
D19s714	7	141	0.894	0.794	0.760	0.588	0.410	0.228	0.075	0.373	ns	-0.0633
C16	9	125	0.912	0.718	0.675	0.688	0.510	0.320	0.122	0.423	*	-0.1352
C19	11	115	0.922	0.814	0.784	0.551	0.375	0.196	0.063	0.360	ns	-0.0666
D1s1665	5	77	0.714	0.657	0.588	0.765	0.611	0.439	0.185	0.470	ns	-0.0539
D2s442	10	64	0.875	0.859	0.835	0.459	0.295	0.128	0.039	0.334	nd	-0.0138
D4S2408	6	47	0.681	0.734	0.685	0.681	0.503	0.316	0.116	0.416	ns	0.0353
Fesps	6	48	0.583	0.679	0.626	0.739	0.566	0.38	0.154	0.453	ns	0.0616
Average	**8.63**	**122**	**0.833**	**0.782**	**0.747**	**0.590**	**0.418**	**0.238**	**0.085**	**0.382**		**-0.0350**

N = number of individuals, k = number of alleles, Ho = observed heterozygosity, He = expected heterozygosity, PIC = polymorphic information content, NE-1P = average non-exclusion probability for the first parent, NE-2P = average non-exclusion probability for the second parent, NE-PP = average non-exclusion probability for a candidate parent pair, P_{ID} = average non-exclusion probability for identity of two unrelated individuals, $P_{ID\text{-}SIB}$ = average non-exclusion probability for identity of two siblings, HW = Tests for deviation from Hardy-Weinberg equilibrium (* = significant deviation, ns = non-significant deviation, nd = not done), F(null) = estimated null allele frequency

Table 3.3a Locus characteristics for adult Phayre's leaf monkeys in the overall population sampled (n=98)

Locus	N	k	Ho	He	HW
D1s207	98	11	0.92	0.88	ns
D1s548	98	9	0.95	0.78	*
D2s1399	98	12	0.94	0.84	ns
D3s1766	98	9	0.87	0.85	ns
D5s1457	98	6	0.85	0.79	ns
D6s1280	98	6	0.82	0.80	ns
D7s1817	98	10	0.82	0.80	*
D10s1432	98	12	0.76	0.70	ns
D11s2002	98	6	0.78	0.74	ns
D13s321	98	8	0.76	0.79	ns
D14s306	98	6	0.87	0.75	*
D17s1290	98	14	0.84	0.85	ns
D19s714	98	7	0.89	0.80	ns
C16	83	9	0.93	0.75	ns
C19	79	11	0.91	0.81	*
D1s1665	56	5	0.66	0.66	ns
D2s442	52	10	0.85	0.84	ns
D4s2408	47	6	0.68	0.73	ns
Fesps	48	6	0.58	0.67	*
Average		**8.9**	**0.85**	**0.79**	

Table 3.3b Locus characteristics for adult Phayre's leaf monkeys in the PA focal group (n=18)

Locus	N	k	Ho	He	HW
D1s207	18	9	1.00	0.88	ns
D1s548	18	8	0.94	0.79	ns
D2s1399	18	9	1.00	0.80	ns
D3s1766	18	7	0.89	0.82	ns
D5s1457	18	6	0.83	0.77	ns
D6s1280	18	6	0.94	0.76	ns
D7s1817	18	8	0.78	0.79	ns
D10s1432	18	10	0.94	0.77	ns
D11s2002	18	4	0.89	0.74	ns
D13s321	18	7	0.72	0.78	ns
D14s306	18	5	0.89	0.75	ns
D17s1290	18	9	0.72	0.81	ns
D19s714	18	6	0.94	0.79	ns
C16	16	6	1.00	0.72	ns
C19	14	6	0.93	0.79	ns
D1s1665	16	5	0.56	0.67	ns
D2s442	16	9	0.88	0.86	ns
D4s2408	17	4	0.59	0.59	ns
Fesps	15	5	0.53	0.63	ns
Average		**6.8**	**0.84**	**0.76**	

Table 3.3c Locus characteristics for adult Phayre's leaf monkeys in the PB focal group (n=16)

Locus	N	k	Ho	He	HW
D1s207	16	9	0.75	0.84	ns
D1s548	16	8	1.00	0.78	ns
D2s1399	16	8	0.88	0.84	*
D3s1766	16	8	1.00	0.82	ns
D5s1457	16	6	0.88	0.74	ns
D6s1280	16	6	0.88	0.80	ns
D7s1817	16	7	0.94	0.79	ns
D10s1432	16	7	0.69	0.61	ns
D11s2002	16	5	0.88	0.72	ns
D13s321	16	6	0.88	0.76	ns
D14s306	16	5	1.00	0.77	ns
D17s1290	16	6	0.94	0.75	ns
D19s714	16	6	0.88	0.77	ns
C16	15	6	0.80	0.72	ns
C19	13	6	0.85	0.77	ns
D1s1665	16	5	0.81	0.66	ns
D2s442	14	9	0.86	0.86	ns
D4s2408	13	6	0.69	0.75	*
Fesps	15	4	0.80	0.62	ns
Average		**6.5**	**0.86**	**0.76**	

Table 3.3d Locus characteristics for adult Phayre's leaf monkeys in the PS focal group (n=9)

Locus	N	k	Ho	He	HW
D1s207	9	6	0.78	0.72	ns
D1s548	9	7	0.89	0.72	ns
D2s1399	9	7	0.89	0.80	ns
D3s1766	9	6	0.89	0.79	ns
D5s1457	9	6	0.89	0.79	ns
D6s1280	9	6	0.78	0.78	ns
D7s1817	9	7	0.89	0.81	ns
D10s1432	9	8	0.89	0.75	ns
D11s2002	9	5	0.89	0.72	ns
D13s321	9	6	0.78	0.77	ns
D14s306	9	4	0.78	0.69	ns
D17s1290	9	10	0.89	0.85	ns
D19s714	9	4	0.67	0.61	ns
C16	9	5	0.89	0.70	ns
C19	9	6	1.00	0.72	ns
D1s1665	9	3	0.56	0.55	ns
D2s442	7	6	0.86	0.80	ns
D4s2408	7	5	0.71	0.73	ns
Fesps	9	4	0.56	0.67	ns
Average		**5.8**	**0.81**	**0.73**	

Table 3.3e Locus characteristics for adult Phayre's leaf monkeys in the PO focal group (n=16)

Locus	**N**	**k**	**Ho**	**He**	**HW**
D1s207	16	9	1.00	0.85	ns
D1s548	16	6	0.94	0.73	ns
D2s1399	16	10	0.94	0.83	ns
D3s1766	16	7	0.88	0.81	ns
D5s1457	16	6	0.81	0.77	ns
D6s1280	16	5	0.94	0.77	ns
D7s1817	16	7	0.88	0.78	*
D10s1432	16	6	0.50	0.57	*
D11s2002	16	4	0.63	0.68	ns
D13s321	16	6	0.88	0.79	ns
D14s306	16	5	0.88	0.72	ns
D17s1290	16	9	0.81	0.77	ns
D19s714	16	6	0.81	0.81	ns
C16	9	5	0.89	0.68	ns
C19	9	6	1.00	0.80	ns
D1s1665	15	4	0.67	0.65	ns
D2s442	15	6	0.80	0.78	ns
D4s2408	10	5	0.80	0.74	ns
Fesps	9	5	0.33	0.70	ns
Average		**6.2**	**0.81**	**0.75**	

Table 3.3f Locus characteristics for adult Phayre's leaf monkeys in the census group (n=39)

Locus	N	k	Ho	He	HW
D1s207	39	9	0.95	0.87	ns
D1s548	39	9	0.95	0.79	ns
D2s1399	39	12	0.95	0.82	ns
D3s1766	39	9	0.79	0.84	ns
D5s1457	39	6	0.85	0.78	ns
D6s1280	39	6	0.69	0.79	ns
D7s1817	39	8	0.74	0.76	ns
D10s1432	39	8	0.77	0.70	ns
D11s2002	39	6	0.72	0.73	ns
D13s321	39	7	0.67	0.77	*
D14s306	39	6	0.82	0.74	*
D17s1290	39	14	0.85	0.87	*
D19s714	39	7	0.95	0.78	ns
C16	34	9	0.97	0.77	ns
C19	34	8	0.88	0.81	*
Average		**8.3**	**0.84**	**0.79**	

Table 3.4 Summary of observed average relatedness across groups by age and sex categories in analysis with groups treated as different populations (n=5)

	All	**All males**	**All females**	**Adults**	**Adult males**	**Adult females**	**Non-adults**	**Non-adult males**	**Non-adult females**
N	9870	820	4950	4753	190	3003	903	210	231
Average R	-0.007	-0.025	-0.010	-0.010	-0.053	-0.013	-0.024	-0.050	-0.048
SE	0.001	0.006	0.002	0.002	0.012	0.002	0.005	0.012	0.012

Table 3.5 Summary of observed average relatedness within groups and census individuals by age and sex categories with groups run independently in analyses

	All Individuals	**Adults**	**Adult males**	**Adult females**	**Adult male-females**	**Non-adults**	**Non-adult males**	**Non-adult females**	**Non-adult male-female**
PA	-0.033	-0.059	-0.365	-0.040	-0.120	0.003	0.011	0.027	-0.016
PB	-0.030	-0.049	*	-0.029	-0.193	0.033	0.048	0.102	0.006
PS	-0.067	-0.127	*	-0.100	-0.219	-0.008	0.026	0.067	-0.055
PO	-0.049	-0.062	-0.017	-0.075	-0.055	0.020	*	0.009	0.038
Census	-0.026	-0.026	0.025	-0.030	-0.031	^	^	^	^
Average	-0.041	-0.065	-0.119	-0.055	-0.124	0.012	0.028	0.051	-0.007

Notes:
* Cells with missing data had only one male in analysis
^ Census data contained only adult individuals

Table 3.6 Summary of tests for sex-biased dispersal among adult and non-adult Phayre's leaf monkeys

		Adults	Adult males	Adult females	Non-adults	Non-adult males	Non-adult females
Overall	**N**	98	20	78	43	21	22
	R	-0.067	-0.119	-0.053	0.038	0.028	0.083
F-statistics	**F_{IS}**	-0.060	-0.066	-0.063	-0.175	-0.125	-0.220
	F_{ST}	0.010	0.029	0.012	0.066	0.049	0.082
	Nm	24.700	8.349	19.917	3.524	4.877	2.802
Assignment Index	**mAlc**		0.041	-0.010		0.050	-0.048
	vAlc		2.946	3.154		2.249	1.777

Table legend:

N = number of individuals
R = Average pairwise relatedness across groups (Queller & Goodnight)
F_{IS} = Inbreeding coefficient
F_{ST} = Population structure (Wright's F-statistic)
Nm = number of effective migrants
mAlc = mean corrected Assignment Index
vAlc = variance in the mean corrected Assignment Index

Chapter 4

Inbreeding avoidance and kin competition drive dispersal and reproduction in female Phayre's leaf monkeys

ABSTRACT

Much theoretical and empirical work has focused on factors affecting patterns of dispersal, including inbreeding avoidance and the reduction competition (for mates or resources). Individual, social, and ecological conditions should be important aspects in understanding dispersal decisions and kin interactions, in particular, could have important fitness consequences. Individuals may increase inclusive fitness by not only staying to cooperate with kin, but also by leaving to reduce competition with either kin or non-kin. This study investigated the influence of kinship and familiarity on female dispersal decisions and reproduction in Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*) in Thailand. We use a demographic database to explore female dispersal (2001-2009) in relation to age and parity, dyadic relatedness ($r \geq 0.125$), and success at reproducing. Inbreeding avoidance and avoidance of kin competition interact to shape female dispersal decisions, although other social and ecological constraints are likely involved. Female emigration is driven by inbreeding avoidance (fathers, brothers and sons) for both natal and secondary dispersers in addition to competition among breeding females. While females enter groups containing female kin, immigration decisions are most likely influenced by avoidance of familiar kin (males and females) and females are more successful at reproducing in groups with unfamiliar females. Thus, while kin-biased affiliative and cooperative behaviors may have important implications for female social

relationships and reproductive success, our results indicate that kin avoidance may also confer fitness benefits, especially for female dispersal species.

INTRODUCTION

Dispersal, or the movement of individuals across space, is a key component in population genetics, regulating gene flow, which in turn influences the genetic structure of a population (overview in Clobert et al. 2001). Dispersal may affect, inbreeding depression (Roze and Rousset 2003, Gandon 1999, Pusey and Wolf 1996), social relationships (Le Galliard et al. 2005, Silk 2002), an individual's life history (e.g., Pen 2000), and speciation (see review in Barton 2001). Dispersal is usually comprised of three stages: (a) leaving an area (or a group), (b) a transient (or roaming) stage, and (c) settling (or immigration; Wright 1969, Clobert et al. 2001, Ronce 2007). It is likely that non-random decisions concerning whether or not to disperse would give an evolutionary advantage compared to a completely random process of dispersal (Ronce et al. 2001). Thus, individual, social, and ecological conditions should be important aspects of dispersal decisions.

It is also important to consider dispersal at both the ultimate and the proximate level (Lawson Handley and Perrin 2007, Long et al. 2008). Ultimate causes of dispersal consider functional and evolutionary questions and, because dispersal is intricately linked to reproduction, it can be viewed as part of a species life history. However, whether or not, when, and to where an individual will actually disperse is determined by the proximate causes of dispersal, which deal with an individual's actual dispersal in a lifetime. Since individuals differ over a lifetime, dispersal decisions are likely to be condition dependent, the combination of which can yield insight into evolutionary causes of dispersal (Hamilton and May 1977, Pusey and Wolf 1996, Gandon and Michalakis 2001, Lawson Handley and Perrin 2007, Long et al. 2008).

Much theoretical and empirical work has focused on three major factors thought to influence patterns of dispersal, including inbreeding avoidance (Pusey and Wolf 1996), reducing mate competition (Moore and Ali 1984) and the reduction of competition for resources (Murray 1967, Bowler and Benton 2005, Ronce et al. 2001). The major factors influencing proximate dispersal decisions are plentiful. Several studies of group living animals have shown the importance of social relationships (e.g., Silk et al. 2003), group size (e.g., Stokes et al. 2003, Pope 2000, Watts 1994), and intrasexual competition (density dependence; Pope 2000, Bonenfant et al. 2009, Clobert et al. 2004, Moore and Rauf 1984) as main causes of dispersal. In addition, however, dispersal decisions are known to depend on the genetic relatedness of individuals within and between groups (Hamilton 1964, Greenwood 1980, Pusey 1987; Clutton-Brock 1989, Pusey and Wolf 1996, Sterck et al. 1997, Lawson Handley and Perrin 2007). For example, kin interactions may lead individuals to stay to increase inclusive fitness through cooperation (Hamilton 1964, Wrangham 1980, Sterck et al. 1997) or to leave to reduce competition either with kin or non-kin (Hamilton and May 1977, Gandon 1999).

For many social mammals and birds, males typically leave their natal group upon sexual maturity and females remain in the same (natal) group throughout a lifetime (Greenwood 1980, Pusey and Packer 1987). Inbreeding avoidance and reducing competition over resources have been suggested to increase the fitness of same-sexed conspecifics often resulting in sex-biases in dispersal (Greenwood 1980, Gandon 1999, Matthysen 2005, Lawson Handley and Perrin 2007, Gros et al. 2008). Long-term studies of non-human primates in the wild have been dominated by species with male-biased dispersal and female philopatry (e.g., baboons, Altmann et al. 1996; macaques, de Ruiter and Geffen 1998; vervets, Cheney and Seyfarth 1983; Hanuman langurs, Borries 2000) in addition to more recent information on African colobines (Harris et al. 2009, Wikberg et al. 2012) and lemurs (Lawler et al. 2003, Morelli et al. 2009). Living in groups with female kin has been suggested to provide females an opportunity to form strong alliances and cooperate with kin. Such female kin alliances have been suggested to help gain access to food resources and to increase fitness (Sterck et al. 1997, van Schaik 1989, Wrangham 1980), which has been supported for some studies of food intake (Koenig 2002) and female reproductive success (Silk 2002, Silk et al. 2003).

In contrast, long-term demographic, social and genetic data on group-living female dispersal species are comparatively rare. While data for chimpanzees (Pusey 1979, Pusey et al. 1997), bonobos (Kano 1992), gorillas (Harcourt 1978; Stokes et al. 2003, Bradley et al. 2007), hamadryas baboons (Sigg et al. 1982), African colobines (Starin 1994, Korstjens and Schippers 2003, Teichroeb et al. 2009, Wikberg et al. 2012), Asian colobines (Poirier 1969, 1970, Rudran 1973, Newton 1987, Kool 1989, Stanford 1991, Sterck 1997, Borries et al. 2004, Chapter 3), Atelids (Symington 1987, Strier 1990, Strier 1994, Crocket and Pope 1993, Ellsworth 2000, Nishimura 2003, Di Fiore and Fletcher 2005, Di Fiore and Campbell 2007), squirrel monkeys (Mitchell et al. 1991, Blair and Melnick 2012), and lemurs (Morelli et al. 2009) are becoming increasingly available, only relatively few studies actually use molecular data to investigate links between female dispersal patterns, kinship and social behavior (i.e., Hohmann et al. 1999, Pope 2000, Stokes et al. 2003, Di Fiore and Fleischer 2005, Morelli et al. 2009, Di Fiore 2009, Di Fiore et al. 2009). Even fewer studies explore these variables in relation to female reproductive success (i.e., Pusey et al. 1997, Pope 2000, Stokes et al. 2003).

In social mammals, female are more likely to disperse in species where male tenure in a group exceeds the time it takes daughters to reach sexual maturity (Clutton-Brock 1989; Clutton-Brock and Lukas 2012). Similar to other social animals, female dispersal in nonhuman primates has commonly been linked to inbreeding avoidance (Moore 1984, Watts 1990, Clutton-Brock 1989, Sterck 1997, Starin 2001, Bradley et al. 2007). However, other social and genetic contexts often remain unknown and context dependent strategies may vary for natal versus secondary dispersers (Pusey and Packer 1987, Pope 2000, Starin 2001, Stokes et al. 2003). Additionally, among female primates infanticide (Watts 1990, Sterck 1997, Crockett and Janson 2000, Stokes et al. 2003) as well as scramble competition (e.g., Wrangham 1980, Jones 1980, Glander 1992, Sterck 1997, 1998, Crockett and Janson 2000) appears to shape dispersal decisions.

Using genetic techniques, previous studies of female dispersal species have shown that individuals may disperse non-randomly and may end up in groups with same-sexed kin (Pope 2000, Bradley et al. 2007, Chapter 3) providing the potential for kin-biased behaviors (Chapais 2001, Bradley et al. 2007, Chapter 3). Preliminary evidence also suggests that nepotistic behaviors among female kin in howler monkeys (Pope 2000) and gorillas (Watts 1994) could potentially enhance female reproductive success despite female dispersal. Similar to most cases of non-random male dispersal in female philopatric primate species (e.g., Cheney and Seyfarth 1983, Jack and Fedigan 2004, van Noordwijk and van Schaik 2001), evidence of non-random female dispersal usually involves cohort dispersal (Starin 1994, Watts 1994, Bradley et al. 2007, Chapter 3) or dispersing into groups consisting of related natal females (Starin 1994, Chapter 3). In addition, despite initial dispersal, female kin groups can develop over time (Pope 2000) or additional social or anthropogenic factors that may lead to groups disbanding (Stokes et al. 2003, Di Fiore 2009, Chapter 3) could result in groups containing female relatives despite female dispersal.

However, living in a group does not necessarily mean living with kin, especially for the dispersing sex (Lukas et al. 2005, Moore 1992). More importantly, having same-sexed kin in a social group does not necessarily translate into a bias towards nepotistic affiliative or cooperative behaviors (e.g., Seyfarth & Cheney 1984, Muroyama 1994, Henzi & Barrett 1999, Silk et al. 1999, Barrett et al. 2000, Langergraber et al. 2007). In fact, biasing relationships towards kin relies on kin recognition or discrimination, which is still debated in the literature (e.g., Blaustein et al. 1991, Holmes & Mateo 2007, Chapais et al. 1997, Rendall 2004). Species in which kin are clustered in burrows or nests, for example, are suggested to develop kin discrimination through association in discrete locations (Blaustein et al. 1987). While experimental evidence shows some support for kin recognition in rodent species (for overview see Pusey and Wolf 1996), for mammals and primates in particular, association or familiarity is the most common explanation of kin recognition (Bowler and Benton 2005) and particularly for a mother and offspring (Holmes and Sherman 1983). While primates are believed to exhibit finely developed kin recognition abilities (Silk 2002), using locational cues for kin recognition is not believed to be as effective for species living in social groups (Hamilton 1987), such as primates. Some support comes from studies that found young monkeys did not discriminate among kin and nonkin during interactions when familiarity was held constant (Erhart et al. 1997; Welker et al. 1987). Most research also suggests that since primates rely on familiarity, they cannot recognize paternal kin (Gouzoules & Gouzoules 1987, Chapais 1995, Mitani et al. 2000). This is because paternal kin are even less evident in most primate species since larger social groups often contain several potential sires and discriminating kin from non-kin would rely on the ability to recognize familial alleles or phenotypic matching. Preliminary studies suggest baboons may decipher individuals that exhibit familial cues (Alberts 1999, Smith 2000) and some evidence shows situation dependent recognition of paternal-kin (Widdig et al. 2001, 2002). However, a criticism of the latter study is that this bias could also result from a preference for age-related cohorts that happened to be sired by a high-ranking male rather than inert recognition (Altman 1979, Rendall 2004). Thus, it seems that when overlapping in a social group, while age similarity and context dependent mechanisms may be important, they may not be the only underlying cues to distinguish kin from non-kin and for paternal kin in particular. To date, the most support for kin recognition among primates is through the mechanism of familiarity with individuals during early development (Rendall 2004).

Despite this progress, it has remained fundamentally unclear to what degree genetic relationships affect dispersal decisions in female dispersal species. Although one of the most widespread factors influencing dispersal decisions is to avoid inbreeding (Clutton-Brock and Lukas 2012), additional circumstances including relatedness to same-sex conspecifics can affect dispersal (Hamilton and May 1977, Gandon 1999, Ronce et al. 2001). In particular, kin competition and kin cooperation have been suggested

(Murray 1967, Hamilton and May 1977, Wrangham 1980, Gandon 1999, Clobert et al. 2001, Ronce et al. 2001, Clobert et al. 2004, Bowler and Benton 2005); however, further information from wild populations are lacking. In addition, how dispersal ultimately contributes to reproductive success is critical to understanding individual dispersal decisions.

This chapter aims to understand the genetic factors influencing female dispersal decisions and reproductive success in wild Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*). This population of Phayre's leaf monkeys from northeastern Thailand shows population substructuring with female dispersal and related males and females within and between groups (Borries et al. 2004, Chapter 3). Since dispersal decisions may differ depending on a female's reproductive condition and relatedness to other females in the group, we consider the following categories for both disappearances/ emigrations and immigrations: (a) natal dispersal, (b) pre-breeding dispersal (non-natal juvenile or nulliparous female) and (c) breeding dispersal (all parous females) in relation to male and female relatives. We explore disappearances and emigrations and how relatedness affects a female's decision to leave, and more specifically whether inbreeding avoidance guides dispersal. If so, we would expect that females are more likely to leave in the presence of related, adult males or males that are near the age of reproduction. To explore the possibility of non-random dispersal and potential for female kin associations, we investigated where and why females immigrate into groups in relation to both male and female relatedness. In addition, we explored the duration of time a female spent in a group in relation to success at reproducing. From the perspective of relatedness (inbreeding avoidance and kin-biased behaviors), we expected (1) that females immigrate into groups with unrelated males, (2) that the presence of female kin influences a female's decision to settle in a group either through kin cooperation or kin competition, and (3) that female reproductive success would be higher in groups with fewer male relatives and more female relatives. In the latter case, females should be attracted to groups with kin, because kin could make good allies (assuming that individuals recognize their relatives). However, if competition for group membership is strong or the costs of dispersal are less than remaining in a group with same-sexed kin, females should avoid groups with kin to avoid the costs of kin competition.

METHODS

Study site and subjects

The study was conducted in Phu Khieo Wildlife Sanctuary, Northeast Thailand (16°5'-35' N, 101°20'-55' E). The sanctuary ranges in elevation from 300 to 1,300 meters above sea level and covers an area of about approximately 1,573 km^2 of dry and hill evergreen forest (Borries et al. 2002, Koenig and Borries 2012). The study site, Huai Mai Sot Yai (16°27'N, 101°38'E), maintains a diverse predator community including diurnal raptors, venomous snakes, large non-venomous snakes including pythons and 30 carnivore species (Grassman et al. 2005, Koenig and Borries 2012). The predation risk for primates is assumed to be high and clouded leopards have been observed in close proximity and even ambushing the study subjects on several occasions (Lloyd et al. 2006).

Four habituated groups (PS, PO, PB, PA) consisting of both one and multi-male organizations of 4 to 26 individuals (Table 4.1, Koenig and Borries 2012) were the main focus of habituation and data collection was from 2000 through 2009. Based on home range size and overlap, density estimates for this population are approximately 1.1 groups/km^2, 16 individuals/group and 20.1 individuals/km^2 (Hassel-Finnegan et al. 2008). Females frequently disperse (Borries et al. 2004, Chapter 3) and may either leave or join groups with unweaned offspring (personal observations, Koenig and Borries 2012). From observations thus far, males either mature to breed in their natal group or leave to form new groups (Koenig and Borries 2012) and genetic evidence shows male gene flow across groups (Chapter 3). The rate of female agonism is relatively low (0.25 interactions per hour) and most interactions consist of displacements over food. Females form linear dominance hierarchies that are potentially age-inversed with young-adult females at the top (Koenig et al. 2004) and dominance rank influences nutritional condition (Chapter 5). In addition, there appears to be some influence on food availability on female reproduction since conceptions are more likely when females are in good physical condition (Lu et al. 2011). This is further supported by group size delayed infant development, delayed weaning, and lower reproductive rates in larger groups (Borries et al. 2011, Chapter 5). The interbirth interval after a surviving offspring is approximately two years on average (Borries et al. 2008) and births occur throughout the year, although there is a birth peak from November to April (Borries et al. 2011, Chapter 5). Infanticide has not been observed in this population.

Demographic and behavioral data collection

Data collection was conducted through behavioral observations of four habituated groups (PA, PB, PO and PS) from January 2001 to January 2009. Group membership varied through death, disappearances, immigration and emigration, births, and, maturation.

Data were derived from regular group contacts, typically all day follows of at least four days per month, for a total of 279 group months or 23.25 group years. In addition, opportunistic contacts and routine infant checks contributed to the dispersal database (Chapters 3 and 5). One additional group, PL, was included due to frequent encounters due to its range between habituated groups (Table 4.1, Figure 4.1). During contacts, we recorded the presence of all individuals with identification based on the shape of the crest, eye rings, muzzle and a depigmented skin area on the lower stomach as well as any scars, injuries, etc. (Koenig et al. 2004). Behavioral observation allowed for identification of mother-offspring dyads, which were later verified via DNA (see below and Chapter 3 for more details).

Ages of individuals were either determined by the known or estimated date of birth or, for older individuals and many of the immigrants, we estimate age by size compared to individuals with a known date of birth (see Appendix 1 for age classes). We consider a female to be juvenile after weaning (on average ca. 19 months of age) until she reaches full head-body length or has her first infant (ca. 5 years of age; Borries et al. 2011, Borries et al. submitted). In addition, here, we classify females by reproductive status including natal, pre-breeding (non-natal juvenile or nulliparous females) or breeding (all parous females) (Appendix 1). This distinction is necessary, because after natal dispersal females may subsequently disperse multiple times before reproducing for the first time (see results).

When a female was no longer found in a group, we distinguished between cases of disappearances (where death or emigration could not be confirmed), temporary absences (up to 90 days) and emigrations (documented transfer to another group). When a female entered a group, we distinguished between temporary presences (less than 90 days), returns (left and returned to group – including natal and non-natal returns) and immigrations (enters a group and stays at least 3 months). The cut-off of 90 days was set based on the distribution of presence/ absence data, i.e., females who stayed (or were absent) for more than 90 days would usually not disperse for several years (or would usually not return).

Upon encountering unknown individuals in the study groups, we would determine sex and age of the immigrant and make an attempt to determine clearly identifiable characteristics and collect a fecal sample. When possible, we distinguished pre-breeding and breeding females using nipple length as well as body proportions as characteristics (Appendix 1). Overall, eight females were classified as unknown or '?' because (1) they were juveniles when we started systematic observations and cannot be classified as natal or pre-breeding, (2) there was only a very brief observation of an individual without clear identification, or (3) fecal samples could not be collected. However, most individuals could be identified individually and even transient individuals could be tracked across the study groups through several dispersal events. This was possible due to the long-term nature of the project, the fact that many of the observers remained in the project for long periods of time, and frequent contact with groups.

Due to the current knowledge of kin recognition, related individuals might not immediately know each other as kin, but rather more likely recognize individuals by familiarity through group membership. Thus, in addition, we distinguished all female-female and male-female dyads as either ‘familiar’ or ‘unfamiliar’. ‘Familiar’ dyads had co-resided at one point in the same study group, while ‘unfamiliar’ dyads had not resided together in a group (natal or otherwise) through the observation period. This classification was restricted to cases for which we had full knowledge of the history of individuals in the study groups.

For immigrating females, we also classified the breeding history in a group as successful or unsuccessful. An immigrant female was considered as being (1) successful - when a female entered a group and stayed there to reproduce or (2) unsuccessful - if a female did not reproduce in a particular group after entering during her residence of over 90 days.

Fecal sample collection and DNA extraction

From 2003 onward, fresh fecal samples were collected noninvasively within a half hour of the time of defecation. Samples were stored using both the one-step (Wasser et al. 1997) and 2-step (Nsubuga et al. 2004) preservation techniques (see Chapter 3 for further details). Samples were collected from most individuals in the 4 habituated groups and at least 3 samples were collected from each individual whenever possible. To obtain a representative population sample, during the primary field phase (2004-2006), fecal samples were also collected from unhabituated groups. Samples were stored at ambient temperature in the field and then shipped back to New York University’s Molecular Anthropology Laboratory for analysis.

Genomic DNA was extracted for 141 individuals that included 102 individuals from habituated groups and 39 individuals from the general population. The DNA extraction protocol followed Qiagen (QIAamp DNA Stool Mini Kit™) procedures with slight modifications (see Chapters 2 and 3). To control for misidentification at the time of fecal collection, at least 2 independent fecal samples (ideally collected by either E. Larney or 2 different field collectors) were extracted for each individual whenever possible.

Microsatellite genotyping

PCR reactions were conducted using Qiagen Multiplex Kits™ following the manufacturers protocols reduced to one-fifth the total recommended volume (10 μl reaction volumes rather than 50 μl; for additional details see Chapters 2 and 3). Each PCR reaction varied in sample subset including a negative and human control. Primers pairs were fluorescently labeled (5' end of either the forward or reverse primer at each locus) and multiplexed when possible (for details see Chapter 2). Amplification conditions used a standard protocol on Bio-Rad thermal cyclers (94 °C for 2 min, 35 cycles of 94 °C for 30 s, 55 °C for 30 s, and 72 °C for 1 min, and a final extension at 72 °C for 5 min) with slight modifications for marker-specific optimization in terms of annealing temperature and number of cycles determined during primer optimization (see Chapter 2).

One microliter of amplified PCR product was diluted up to 1:20 in formamide to which a commercially available fluorescent size standard (ROX 500) and separated using electrophoresis (ABI 3730 Automated DNA Analysis System) using Gene Mapper software (Applied Biosystems) and alleles were sized by eye. Individuals were genotyped at between 15 to 19 polymorphic loci (Chapters 2 and 3) and all individuals were genotyped using at least 2 replicates for heterozygotes and at least 7 replicates for homozygotes (Taberlett et al. 1996, Morin et al. 2001, Chapter 3). In addition, known mother-offspring dyads were checked for allelic mismatch whenever possible.

Genetic and behavioral analysis

The loci characteristics, genetic structure and dispersal pattern of this population of Phayre's leaf monkeys are presented in detail elsewhere (Chapters 2 and 3). Dyadic relatedness values (pairwise coefficients of relatedness or "r-values") were derived for the population using likelihood ratios between hypothesized pedigree relationships using the regression-based Queller and Goodnight relatedness estimator (Queller and Goodnight 1989) through the program GenAlEx v. 6.501 (Peakall and Smouse 2006). The pairwise coefficient of relatedness (r) was calculated for all dyads of individuals for which genetic data were available and dyads were considered related at $r \geq 0.125$, and parent-offspring dyads were considered related at $r \geq 0.5$ (Queller and Goodnight 1989) and from previous paternity analysis (Chapter 3). Dyadic relatedness was compared for all individuals within a group up to one month prior to a dispersal event.

Statistical tests followed standard procedures as described in Sokal and Rohlf (1995) and Siegel and Castellan (1988). Descriptive statistics were run using SPSS (version 19) and tests were carried out using an alpha level of 0.05. We used a G-test for independence to explore emigration and immigration in breeding versus non-breeding females. We used a G-test for goodness of fit (applying Williams's correction) to explore female emigration from and immigration into groups relative to relatedness of individuals (male and female) in the group. We used a Fisher's exact test to compare the number of related and unrelated males or females for females that remained in a group for long- versus temporary tenure. We used a binomial test to determine if immigration events were related to the presence of familiar and unfamiliar female kin and to see if a female's success at reproducing was related to female kinship or familiarity. We used a logistical regression to explore whether a female's reproductive status (breeding versus pre-breeding, variable 1) and the presence or absence of male kin (variable 2) were predictive of female tenure in the group (<90 days coded as 0, >90 days coded as 1).

RESULTS

Overall we observed 141 dispersal events including 80 cases of disappearances, temporary absences and emigrations as well as 61 temporary presences, returns or immigrations.

Disappearance, Temporary Presence and Emigration

The 80 observed cases of disappearances, temporary absences and emigrations included breeding, pre-breeding, and natal females (Table 4.2). Overall, focal groups lost females at a rate of 3.4 events per group-year consisting of 1.8 disappearances, 0.3 temporary absences and 1.3 emigration events. Since confirmation of the whereabouts of individuals leaving a group is difficult to observe in the wild, it is not surprising that the majority of our cases (52.5%) involved female disappearances. In 10% of the documented events, Phayre's females were observed to temporarily leave groups, in that a female was absent from a group ranging from a few to up to 90 days. While temporary absences were less frequent compared to disappearances or emigrations, it is notable that females in all reproductive categories were documented to leave and return and females temporarily left a social group before returning for 33.4 days on average (range 1 day to 80 days). Confirmed female emigration, where a female left and entered another group, was documented in 37.5% of the cases. There were two cases in which a female left and then returned to the same group after a comparatively long time (mean of 297.5 days) and thus were considered within the emigration category.

In general, the majority of cases (71%) in which females left focal groups involved juvenile females (natal and pre-breeding, n= 57 confirmed events), with pre-breeding females being the most frequent age-class to leave (41%). Juvenile females leave at around 4 years of age on average, approximately a year before the average age of first reproduction (5.3 years of age; Borries et al. 2011). Given that adult females are more numerous in the population, we found that juvenile dispersal (natal and pre-breeding) occurred significantly more often than expected by chance (G_{adj}=34.82, df=1, P<0.001). However, secondary dispersal of breeding females is also common in this population with 21 out of 80 cases (26%) and only slightly less frequent than natal dispersal (24 events). Secondary dispersal takes place at a rather young age of about 8-9 years of age; however, this is likely an underestimate given that the age of older females is usually unknown.

For the 60 cases in which genetic data were available for disappearances, temporary absences and emigrations, the subset (75%) was representative of the overall database (Figure 4.2). Again, disappearances, temporary absences, and emigrations were most frequent in pre-breeding females (natal and pre-breeding), which constitute almost half of the cases (47%). Events involving breeding females occurred almost half as often (25%) compared to non-breeding females, but only slightly less than natal females independently (Figure 4.2).

Emigration and Male Relatives

Given that female dispersal is often guided by inbreeding avoidance, we expected that females are more likely to leave in the presence of related adult males or related males near the age of reproduction.

Male kin were present in 62% of all cases of female disappearances, temporary absences, and emigration (n=60; Table 4.3). Except for PL, which had an atypically small group size, related males were otherwise present in all focal groups (Figure 4.3). Overall, females in groups containing more males on average (e.g., PA and PO, Table 4.1) had fewer male relatives present. When exploring the distribution of male kin in relation to female demographic classification (Table 4.4), related adult males were present slightly more often (48% of the time; 29 of 60 events) than related non-adult males (40% of the time; 24 of 60 events) and both adult and non-adult male kin occurred across breeding, pre-breeding and natal females (Figure 4.4).

Overall for the cases in which male relatives were present (n=37, Table 4.4), 78% of these included an adult male relative and 65% a non-adult male relative in the group. Given that adult females should be more numerous in the population, we found that the presence of male relatives was significantly different for the 3 reproductive categories (G_{adj}=20.12, df=2, P<0.001). However, 23 cases (38%) involved females leaving despite unrelated males being present, indicating that inbreeding avoidance may not be the only reason for non-natal dispersal. Pre-breeding females had the most unrelated males when leaving groups (70% of the 23 cases when no male relative was present), while natal females always had a male relative when leaving, often the father or a brother. Breeding females had sons in the group. Although demographic history was not known earlier than 2001, in almost half of the overall cases in which a female left a group (46%), the related male was likely not from the female's natal or breeding group (breeding and pre-breeding) and, thus, it was unlikely that these females knew that the male relative was kin.

Adult male kin were present in almost half (48%) of all cases of female disappearance, temporary absence and emigration (Table 4.4) and were represented across all female demographic categories. In 8 of the 29 cases in which adult male kin were present (28%), the adult male relative was the sole adult male in the group. While adult male kin were present in both one and multi-male groups, there were no cases in multi-male groups in which a female had more than one adult male relative (e.g., there was always another unrelated adult male present in multi-male groups) and sole adult male relatives only involved natal and breeding females. Most cases involved natal females (75%, 6 of 8 cases) that were familiar that the sole adult male was her kin since it involved her father (n=5) or paternal kin (n=1). Interestingly, however, there were 2 cases in which breeding females also had a sole adult reproductive male in her group. However, both of the cases for breeding females followed a turnover or disbanding of male group membership prior to the period in which the female left. The presence of non-adult male kin was also frequent (40% of all events), with two cases in which a female left a son in a group, six cases where a female left a non-adult maternal brother, and another 15 cases involving other paternal male kin remaining in the group.

As expected, in all cases of natal dispersal, male kin were present and these included both fathers (14 cases) and maternal brothers (1 case for adult males, 6 cases for non-adult males). In 15 cases of natal dispersal the related male was adult, and in 6 of these it was the only adult male in the group. In addition, there were 7 cases for natal females that included leaving a group in which her maternal brother was present (5 of which her father was also present) and 1 case (B7.1) in which other natal paternal kin were present. Male relatives were also present in over half of the documented cases for breeding females (53%, 8 of 15 events), including 6 cases of adult male relatives and 4 cases on non-adult male relatives. Several cases, however, were not mutually exclusive, e.g., there may be a related adult and non-adult male present at the same time. For three breeding females, the male relative was her son (1 adult and 2 non-adult). In three additional cases, there were other natal non-adult male kin in the group. Interestingly, there were 12 cases in which pre-breeding females also had male relatives in the group for which demographic observation (e.g., no known fathers or brothers) indicate they likely had no knowledge of these males as relatives.

Emigration and Female Relatives

To explore if female kinship might have an influence as to whether or not a female stays or leaves a group, we looked a female's dyadic relatedness in relation to the other adult and juvenile females that were in the group just prior to the time she left. For 60 of the 80 documented disappearance, temporary absence or emigration events (74%)

we had genetic and complete demographic data available to explore this further. Table 4.5 summarizes the overall findings. Other than the PL group that had an uncharacteristically small group size prior to fusing with one of the other social groups (Koenig and Borries 2012), female kin (both adult and non-adult) were present in all focal groups prior to a female's departure (82-100% of cases; Table 4.5, Figure 4.5). Adult female relatives were more frequent than non-adult female relatives for all social groups except PO, where there were more non-adult females than adult female kin present. In 82% of the cases, adult female kin were present at the time a female left. The majority of cases of related adult females did not exclusively include a mother as the adult female relative, yet other related adult females (90%). Only 5 cases (10%) included females leaving a mother as the only adult female relative in the group. In addition, in 57% of the cases overall, related non-adult females were also present.

Overall, in 92% of the cases females left groups despite having female kin present across the three dispersal categories (Table 4.6). As expected, natal females always (100%) had female kin present in the groups they left, followed by breeding females (in 93% of the cases for breeding females) and pre-breeding females (86% of the cases for pre-breeding females). Even after excluding cases for natal females that automatically bias the dataset towards kin being present, we did not find that the presence or absence of female kin was different between breeding and pre-breeding females that left groups (Fisher test, p=0.643).

Immigration

Overall, we documented the temporary presence, return or immigration of a total of 61 events (Table 4.7). We observed immigrations of both juvenile and adult females at a rate of 1.2 events per group year with the majority of cases involving juvenile females (43 out of 61 individuals). In almost half of the cases (44%), females were not necessarily staying in the group they entered and these temporary visits (n=27) also occurred at a rate of 1.2 events per group year. In these cases, females were often only present for some days or weeks, with an average stay of 25 days or just under one month (range 1-76 days). In addition, some females (n=5) left and returned to the same group. Overall, we observed 2.6 females enter a group per group year. Just over half (56%) of the females that come into a group stayed for longer.

Our definition of immigration requires that a female stayed in a group longer than 3 months; however, this did not necessarily mean that the female reproduced (referred to as 'successful'). We could document a total of 16 cases (or 26% of all events) including both secondary and natal/ pre-breeding dispersal in which females came into a group and reproduced (an additional 4 cases remained open because of the end of the study).

In 52 cases, genetic data was available for temporary presences, returns and immigrations (85%). This information was representative of the overall database (Figure 4.6). The genetic subset comprised of 52% immigrations at a rate of 0.9 females per group year, 42% temporary presences at a rate of 0.1 females per group year and 6% returns (natal and non-natal) at a rate of 1.2 females per group year and 31% (16 of 52) with successful reproduction.

Immigration and Relatedness to Males

To explore whether or not inbreeding avoidance guided which group females chose to enter and stay in, we compared a female's relatedness to the males residing in the group they entered. Overall, females joined groups (temporary presence, return, and immigration) slightly more often when related males are not present (56%, n=29), but are also found to enter groups containing male relatives in 23 cases (Table 4.8). Considering all observed events in which females entered focal groups, male relatives were present in all groups except for PL and male kin consisted of both adults and non-adults (Table 4.8, Figure 4.7). As would be expected by chance alone, females entering groups containing fewer males (PB, PS and PL) had a greater chance of overlapping with male relatives. Related males were present in 44% of the observed events in which females entered a group on average, and this consisted of adult male kin only slightly more often than non-adult male kin (Figure 4.7).

The proportion of related versus unrelated males did not vary when comparing females that temporarily entered or returned to groups (<90 days) compared to longer-termed returns and immigrations (>90 days) overall (G_{adj}=0.23, df=1, p>0.05) as well as independently within each of the three reproductive categories (Table 4.9, Figure 4.8). There seems to be some indication that breeding females that stayed longer in groups have fewer male kin in groups, however the sample size is small and the difference non-significant (Fisher, p=0.286). For females that temporarily joined groups (<90 days), groups' contained male kin only slightly less often (45%) than chance and females had equal chances that the male kin were adult (50% of the short-term cases) or non-adult (50% of the short-term cases). For cases in which a female resided in a group longer-term

(>90 days, n=30), male kin were still present just under half the time a female entered a group (43%), including adult males (40% of the long-term cases) and non-adult males (23% of long-term cases). While females had adult male kin across each of the demographic categories, juvenile females constitute the majority of cases of entering groups with related males (both adults and non-adults; Table 4.9) and had a 50:50 ratio of related versus unrelated males as expected by chance. Overall, for the 13 cases in which related males were present for long-term resident females, this consisted of adult male relatives on 12 accounts (92% of cases where male relatives were present) and non-adult male kin in 7 cases (54% of the time there is a male relative).

We further combined the data to explore the potential differences between breeding (secondary) dispersal versus pre-breeding (pre-breeding nulliparous adult and juvenile females). In this case, we omitted the two instances of natal returns, as this automatically biases the sample size towards kin. The overall presence or absence of male kin across types of immigration did not change the results (compare Table 4.9 and 4.10). Male presence or absence seemed not to differ.

This was confirmed through a logistical regression, which did not find that female reproductive status or presence of male kin affected female tenure after entering groups (Table 4.11). In addition, our results show that for younger females (pre-breeding) the odds of staying in groups longer-term are about 6.3 times greater than breeding females controlling for presence/absence of male kin. Females with male kin present have much lower odds (1.0) of staying long-term compared to females without male kin present when controlling for reproductive state (breeding vs. pre-breeding).

Immigration, Relatedness to Males and Reproductive Success

Overall, females were only slightly more successful (63%) than unsuccessful (53%) at reproducing in a group without the presence of male relatives (Table 4.12). In 6 cases females bred successfully in groups with related males present. There was no significant difference in reproduction whether or not related males were present (Fisher's test, p=0.758). This result did not change when natal females were excluded (Table 4.13, Fisher test, p=0.762). Furthermore, it did not change if only longer-term presence of females was considered (Table 4.14; Fisher test, p=1.0). Taking just immigration (over 90 days) from closed cases in which reproduction status was confirmed, females reproduced in the same proportion in groups with unrelated (63%) or related males present (27%) than females that did not reproduce (Table 4.14, Figure 4.9).

When looking more closely at only the cases where females stayed in a group to reproduce (n=16, Table 4.15), females are successful at reproducing in the absence of male kin in 10 out of 16 cases (63%). Our results indicate that pre-breeding females have a high chance (50%) of entering and staying to reproduce in a group containing male kin compared to breeding females (only 1 case, 17%). Surprisingly, in five of our successful cases, there were also adult males present. However, it remains to be determined if the females actually reproduced with male relatives.

While females may consort with male relatives, these males are likely unfamiliar and there was almost always a non-related male also in the group (excluding one female mentioned above). It seemed, however, that familiarity of male relatives might be an important factor. In fact, females appeared to avoid familiar male kin in 49 of the 52 cases (49 cases unfamiliar males versus 3 cases entering a group with familiar male relatives). More importantly, in none of the 52 events did a female stay to reproduce in a group with familiar male kin.

Immigration, Relatedness and Familiarity to Other Females

Females were immigrating into groups with female relatives in 83% of cases (43 of 52 cases), primarily consisting of events involving juvenile females (32 of 52 cases). Female kin are present in 71-92% of the cases per group (excluding PL; Table 4.16) and there was no significant difference in the ratio of related to unrelated females across groups. For all groups except PL, both adult and non-adult female kin were present, and usually adult female relatives were slightly more common than non-adult female relatives. In none of the cases did a female (natal or otherwise) return or enter a group that her mother was residing in.

Excluding natal female returns, the dataset included a total of 50 cases of immigrations, temporary presences and returns including 22 short-term presences (<90 days) and 28 long-term immigrations (over 90 days; Table 4.17). Females were entering into groups with other female kin in 41 of the 50 documented events (82%), including groups containing adult female kin (68%) as well as non-adult female kin (44%). There was no significant difference between breeding categories in the number of female kin present (Fisher test, p=0.595) nor when comparing female kin versus non-kin in short-term visits versus long-term immigrations (Fisher test, p=1.0). When comparing breeding females to all non-breeding females (pre-breeding and juvenile) (Figure 4.10), we found that non-breeding females (84%) immigrate into groups with female kin slightly more often than breeding females (71%). Breeding females also tend to have even fewer female relatives in a group (67%) compared to non-breeding females that have slightly more female kin (86%) for longer-termed returns or immigrations (>90 days). In general, females entered into groups with other adult female kin in 34 out of 50 cases (68%) compared to groups containing non-adult female kin (44%). Breeding females have slightly more adult female relatives when they enter a group (71%) compared to non-breeding females (67%), although this difference is slightly less evident the longer breeding (67%) and non-breeding (64%) females stayed.

Due to long-term behavioral observations, we were able to further differentiate whether a female was likely unfamiliar or familiar with the female kin in the group she was entering. Looking at all cases of female immigration, return and temporary presence in relation to familiarity, we found that females appear to enter into groups with unfamiliar related females significantly more often than familiar related females (Table 4.17; 31 versus 10 cases, Binomial, $p<0.005$). From the 50 observed immigration events, unrelated females were present in 9 cases, female kin in 31 cases and familiar female kin in 10 cases. However, there was no significant difference overall between the number of familiar and unfamiliar female kin in groups dependent on a female's tenure (Fisher, $P=0.467$). Unfamiliar female kin were present in 15 short-term presences and 16 long-term immigrations or returns. The chances of groups containing familiar female kin does appear to increase slightly with tenure, with 3 cases for females entering groups for a short-term compared to 7 cases for females entering groups longer-term (including 14% versus 25% of all related females, respectively). Overall, the percentage of familiar adult female kin remained the same despite tenure (14%), whereas familiarity of non-adults decreased slightly as female stayed longer in groups. Breeding females never were observed to enter groups with familiar female kin, while non-breeding females did. Non-breeding females entered groups with familiar *adult* kin only slightly more often when adult female kin were present (7 out of 29 cases or 24%) than familiar *non-adult* kin (4 of 20 cases when non-adult female kin were present or 20%). Non-breeding females had a slightly higher chance of being in a group with familiar related adult females the longer a female stayed (3 of 15 events in the short-term or 20% versus 4 of 14 long-term immigrant events or 29%). However, non-breeding females tended to enter and stay in groups with familiar non-adult female relatives in 20% of the cases despite tenure.

Immigration, Female Relatedness, Familiarity and Reproductive Success

For all longer-term immigrations and returns (>90 days), we found that a female's success at reproducing was relatively similar whether or not female kin were present in the group (Table 4.18, Figure 4.11a; Fisher test, p=0.262). Overall, female kin were present in 23 out of 28 events (82%) and 20 out of 24 closed cases (83%). Females were successful at reproducing in 16 of the 24 closed cases overall (67%), including 12 out of the 24 closed cases with female kin present (50%), 9 of the 24 cases (38%) with adult female kin and 7 of the 24 cases (38%) with non-adult female kin. For females that left groups prior to reproducing, all 8 cases (100%) involved females leaving a group containing female kin.

Judged by familiarity with kin, females were only successful at reproducing in groups containing familiar female kin in 2 of the 24 closed cases (8%; Fisher test, p=0.289; Table 4.17, Figure 4.11b). In only 2 out the 16 cases where females successfully reproduced, they did so in the presence of familiar kin (14%; Binomial test, p<0.005;

Table 4.17). From closed cases of reproduction with female kin present (n=20), familiar female kin were present in 5 of 20 cases (25%) with female relatives, familiar adult female kin in 3 of the 15 cases (20%) with related adult females and familiar non-adult kin in 2 of the 12 cases (17%) with related non-adult females. For cases in which female relatives were present, females were successful at reproducing only 10% of the time (2 out of 20 cases overall and 2 out of 15 cases for adult relatives), although a female never reproduced successfully with familiar, non-adult females present (0 out of 12 cases).

Looking more closely at the 16 successful cases of reproduction (Table 4.19, Figure 4.12), overall pre-breeding females (10 out of 16 cases) were almost twice as likely to reproduce in a group than breeding females (6 out of 16 cases). While female kin were present in groups 75% of the time (12 out of 16 cases), breeding females had significantly fewer female relatives (4 of 16 cases or 25%) compared to pre-breeding females (8 of 16 cases or 50%). Overall however, breeding females still had female kin in groups in which they reproduced over half of the time (4 of 6 cases; 67%) and this was even more pronounced for pre-breeding females (8 of 10 cases; 80%). Breeding females had double the number of adult kin (n=4) compared to non-adult kin (n=2); however, none of these female kin were familiar. Pre-breeding females, on the other hand, had an equal number of cases with adult and non-adult kin (n=5 in both cases), and included the only two cases in which a female immigrated and reproduced in a group with familiar female kin.

DISCUSSION

Disappearances, Temporary Absences, and Emigrations

In this study, we were able to document 80 cases of female disappearances, temporary absences and emigrations at a rate of 3.4 events per group-year. This information supports previous findings (Borries et al. 2004, Chapter 3) that female dispersal is quite common in Phayre's leaf monkeys. It is presumed here that most cases involving female disappearances were likely followed by (missed) immigration events. Typically, secondary dispersal involved younger breeding females that still had long-term reproductive potential afterwards. Most other females that left after having offspring either did so with their dependent offspring, after an infant had died, or closer to mean weaning age of infants in this population increasing the potential for its survival or after an offspring was weaned (Borries et al. 2008). Similar to what has been reported in western lowland gorillas (Stokes et al. 2003), the death of an infant can be an important driver in female secondary dispersal.

There was also some evidence, however, that Phayre's females only temporarily leave groups and it is notable that females in all reproductive categories were documented to leave and return. Although the social contexts are discussed elsewhere in more detail (Koenig et al., in prep), this does provide some indication that unlike howler monkeys (Pope 2000, but see Ellsworth 2000), aggressive female eviction was not always the proximate reason for a female's decision to leave since returning females were observed to enter with relatively little aggression and some females came and left multiple times and this did not always involve natal females (e.g., A14, A15 and A17). While agonistic relationships and the development of social ties with resident females may be important factors in a female's potential for long-term group membership and reproductive success (Chapter 5, Koenig et al, in prep), it seems that certain primates exhibit more flexibility when transferring between groups as seen in Temminck's red colobus (Starin 2001) and Thomas langurs (Sterck 1997). When a female finds the potential to leave may outweigh staying (e.g., especially following intergroup encounters), Phayre's females appear to "test" groups to potentially weigh the costs and benefits of leaving permanently and these visits can sometimes range from several days to almost a year.

Largely due to the long-term nature of the dataset (Koenig and Borries 2012) and considering the comparatively high rate of dispersal and large dispersal landscape (Borries et al. 2004, Chapter 3), we were also able to confirm a relatively high percentage of events as female emigrations. Similar to what has been described in other female dispersal species (e.g., Harcourt 1978, Pusey 1980, Mitchell et al. 1991, Glander 1992, Sterck 1997, Printes and Strier 1999, Starin 2001, Teichroeb et al. 2009, Clarke and Glander 2010), we found the majority of cases in which females left focal groups involved juvenile females. However, it was interesting that most cases actually involved pre-breeding, non-natal females. It is possible that our findings could be a result of a greater tendency for non-confirmation of natal emigration cases (classified here as disappearances) due to the dispersal distance since long-term observations were primarily focused on four main neighboring focal groups and natal females likely display a greater dispersal distance. Juvenile females leave approximately a year before the average age of first reproduction (Borries et al. 2011), which could potentially provide females time to test groups and develop social relationships with both males and females prior to settling and reproducing. Similar to temporary absences in Phayre's females, documented emigrations provide even stronger support for secondary dispersal of breeding females as well, although breeding females still tend to be rather young. Secondary dispersal seems to be rather common in female dispersal species, although species-specific causes appear to vary (Starin 1991, Stokes et al. 2003, Morelli et al. 2009, Di Fiore 2009).

Interestingly, we also documented two cases of females having left and then returning to the same group after almost a year. While immigration and reproductive success is discussed in more detail below, this does provide the insight that a transient state can be quite long in duration for some females and further supports female secondary dispersal. In addition, this could also contribute to further explanation of the genetic structure of this population since a long hiatus could provide opportunities for extra-group copulations as suggested elsewhere (Chapter 3, Koenig et al. unpublished).

Female Emigration: Inbreeding avoidance

There is substantial support for inbreeding avoidance as a main cause of dispersal decisions for other animals, which usually leads to a sex bias in dispersal (Greenwood 1980, Pusey and Wolf 1996, Gandon 1999, Matthysen 2005, Lawson Handley and Perrin 2007, Gros et al. 2008). Given that this population exhibits frequent female dispersal (Borries et al. 2008, Chapter 3), the question was whether inbreeding avoidance guides dispersal across females and how this varied, if at all, by a female's age and reproductive category. If inbreeding avoidance could be a cause of dispersal, females should be more likely to leave a group with the presence of related males who are at or near the age of reproduction and this would be most common for natal females (Greenwood 1980).

We found that related males were present across groups for both transient and longer-tenured females around 60% of the time, including both non-adult and adult males. In addition, we found cases of male relatives present across all female reproductive categories (natal, pre-breeding and breeding) when a female was documented to have left a group. At first, this seems to suggest that inbreeding avoidance is not of major importance in this population. However, several lines of evidence suggest that it is driving some of the female's decisions to disperse.

As expected, natal females always had a male relative present, usually her father or brother, in the group. If a natal female had an elder brother, she always left before he reached sexual maturity (sub-adult age). In fact, for the only natal female who reproduced in her natal group (A7.1), her presumed father (M2) had disappeared from the group when she was a juvenile and she did not have any other male relatives in the group. For breeding females, however, the situation is slightly different because the related male is often her maturing son. Unexpectedly, there were 12 cases in which pre-breeding females, which should not have paternal kin or offspring present. However, demographic observations likely indicate that these females were unfamiliar that these males were relatives (e.g., non-natal, non-father). Thus, inbreeding avoidance seems to have a strong influence on dispersal decisions for natal and breeding females.

Not surprisingly, females left groups with a relatively high percentage of adult male kin, or potential reproductive partners, rather than non-adult male relatives. However, although complete demographic histories were not known for all individuals prior to 2001, it is likely that almost half of the cases in which a female left a group, the related male was not from the female's natal group (breeding and pre-breeding) and, thus, it was unlikely that these females were familiar with these males (it remains unclear whether any mechanism of kin recognition exists). Similarly, Sterck (1997) did not find a connection between the lack of unrelated reproductive males with the timing of female transfer in Thomas langurs. At the same time, while adult males were frequently present in groups prior to a female's departure, there was always at least one unrelated adult male present in multi-male groups. Nonetheless, it seems that in some cases, the lack of reproductive partners might be influencing female dispersal decisions. As described in mountain gorillas (Stokes et al. 2003), muriquis (Strier 1994) and other New World monkeys (Di Fiore 2009), group male turnovers or disbanding might be an important influence to some Phayre's females decisions to leave. The presence of non-adult male relatives was also frequent, where females left groups with sons, brothers or other paternal kin prior to sexual maturity.

Due to both natal and secondary female dispersal, there are several ways in which a male relative would end up in a group aside from natal group female-male relationships. In fact, we have found that females both temporarily and permanently leave groups with dependent offspring (Larney, personal observation; Koenig and Borries 2012). In addition, a female could reproduce in one group, secondarily disperse and then reproduce in another. Hypothetically, if the first offspring (female) happened to disperse into the same second group as her mother (who had successfully reproduced in that group), then there could be a half-sibling present. Also, although it still remains to be confirmed, some females could potentially mate extra-group copulations (paternity analysis confirms that not all infants are necessarily sired by the resident male, Chapter 3). Thus, with female Phayre's complex and somewhat fluid dispersal system, a female could potentially end up in a group with either a related male or female, with our without previous knowledge of that individual. However, it is also plausible that a female would not necessarily have to leave and could remain in a group with male relatives as long as there is at least one non-kin male to potentially breed with, as suggested in woolly monkeys (Di Fiore 2009) and Milne-Edward's sifakas (Morelli et al. 2009).

Similar to what has been described for other primate species in which females disperse (Pusey 1980, Starin et al. 1991, Pope 2000, Sterck 1997, Stokes et al. 2003, Bradley et al. 2007, Morelli et al. 2009, Di Fiore 2009, Teichroeb et al. 2009), our results show that inbreeding avoidance is an important factor for both natal and secondary dispersal in female Phayre's leaf monkeys. However, 23% of cases in which a female left a group involved females leaving despite unrelated males being present, indicating that inbreeding may not be the only reason for non-natal transfers. Additional evidence suggests that social contexts involving males may also influence if and when a female decides to leave. Similar to what has been reported for gorillas (Stokes et al. 2003) and for spider monkeys (Di Fiore 2009), it is possible that group disbanding could influence some female decisions to leave. Our study shows potential evidence of this in at least three study groups (PB, PO, and PL; for more details see Koenig and Borries 2012) and a female may leave with or without certain group males' and/ or females. In addition, observations indicate that changes in male status (e.g., rank or reproductive) may also influence secondary dispersal, since some well-studied females (e.g., All, B10) were observed to leave after a longer-tenured alpha male changed, although other intra-sexual social factors may have been involved. From observations, it seems that infanticide avoidance from either males (e.g., van Schaik 1989, Sterck 1997, Stokes et al. 2003, Morelli et al. 2009, Teichroeb et al. 2009) or even females (e.g., Morelli et al. 2009) may not be as influential a factor in dispersal decisions of Phayre's females. Infanticide has never been observed in this species and more importantly, females sometimes transferred between groups with dependent offspring, unlike what has been observed in other species that found female transfer closely linked to infanticide avoidance (e.g., red howler monkeys, Crocket and Pope 1993; Thomas langurs, Sterck 1997; western lowland gorillas, Stokes et al. 2003; ursine colobus, Teichroeb et al. 2009). Thus, in addition to inbreeding avoidance, it seems likely that other variables (genetic or social) might also influence the dispersal pattern in female Phayre's leaf monkeys. Considering males alone – group stability may also play an important role in a female's decision to emigrate.

Female emigration: Social and ecological constraints may outweigh the potential benefits of same-sex kin associations

Previous evidence for nonhuman primates and other animals suggests that nepotism may shape same-sex social relationships (Sterck et al. 1997, Silk 2002) and may even be important for the relationships among the dispersing sex (e.g., Crocket and Pope 1993, Watts 1994, Wikberg et al. 2012). Contrary to what would be expected if kin selection were driving females to stay and cooperative with kin, we found that in 92% of cases, females left groups despite having female kin present. Related females (both adult and non-adult) were present across all of the focal groups that females left, except for PL that has an atypically small group size.

Adult female relatives were more frequent than non-adult female relatives for all social groups except PO, where there were more non-adult females than adult female relatives present. In 82% of the events, related adult females were present at the time a female left. While we might expect that adult females (e.g., mothers) might be present and potentially affecting dispersal decisions as documented in howler monkeys (Pope 1998), most cases of related female adults did not exclusively include a mother-daughter dyad but other related adult females. In fact, only 5 cases of adult female relatives included a mother as the only adult female relative in the group. In all cases where a mother was present, however, females were observed to leave if she was still residing in the group. In addition, there was only one case (S2.2), where a female's maternal sister was the only adult female relative in the group. We also found that in over half (57%) of the cases with female relatives, related non-adult females were also present. Thus, despite the potential for kin alliances and cooperation, even non-natal Phayre's females are leaving groups despite the presence of female kin. From other observations it is known that, in addition to inbreeding avoidance, several social influences likely influence a female's decision to leave. In particular, it appears that large group size (Borries et al. 2008), agonism by other females, male turnovers, and unsuccessful reproduction may influence when a female may leave (Koenig et al., unpublished). Such social and ecological costs may outweigh potential the benefits of female kin associations within the group (Isbell and van Vuren 1996, Bradley et al. 2007, Teichroeb et al. 2009, but see Mitchell et al. 1991). This, together with the dispersal away female from relatives, seems to indicate a strategy of avoidance of kin competition.

Immigration

We were able to document the temporary presence, return or immigration of a total of 61 events for Phayre's females at a rate of 2.6 events per group year. We observed immigrations of both juveniles and adult females, with juveniles being observed to enter groups significantly more often than older females (consistent with the results for emigrations). Temporary presences of females in a group were observed at a rate of 1.2 events per group year and returns (both natal and non-natal) were observed less often at a rate of 0.2 events per group year. Just over half of the females that came into a group (56%) stayed longer than 90 days and documented female immigration was observed at a rate of 1.2 events per group year. Several females (both natal and non-natal) were also observed to come and go between groups rather frequently. Although, when breeding females transferred between groups this was usually longer-term. Within these records, we have been able to document 16 cases in which females came into a group and reproduced. Reproduction was documented for both natal/ pre-breeding and secondary dispersal.

Female Immigration and Reproduction: Inbreeding avoidance and chance encounters

Overall, females joined groups with both related and unrelated males. In most observed events, a female went into a group with male relatives; however, these were often either a return to her natal group or transfer into a group with male kin she was likely unfamiliar with. Since this population does not exhibit a high level of inbreeding, it is possible that females ended up in a group with a male relative by chance (see discussion elsewhere and more details in Chapter 3) and other male attributes and/ or genetic or social attributes of females or ecology may be more influential on a female's decision to enter a group. Overall, as would be expected by chance alone, females entering groups containing fewer males had a greater chance of overlapping with male relatives.

Females reproduced in groups with unrelated males present only slightly more often than expected by chance. As discussed above, the presence of related (and possibly unfamiliar) males can occur in this population through various mechanisms. Thus, it is possible that females cannot avoid male relatives despite the question of whether they can actually recognize kin. Alternatively, females may still enter or return to groups with known male relatives, but opt not to breed with them. In fact, there was only one case in which the adult male was the only adult male in the group (although likely unfamiliar). Thus, while the presence of related males seems almost unavoidable, females still have the potential to breed with unrelated males (and as seen in other species, females may stick around as long as there is a non-related male around to breed with, e.g., Morelli et al. 2009). Whether or not females then breed with these male relatives is still undetermined (Larney, unpublished).

Overall, female Phayre's leaf monkeys often ended up entering and staying in groups despite the presence of male relatives. Our results indicate that juveniles have a 50:50 chance of male kin being present or absent and pre-breeding females also seem not to select group based on the presence of male kin or are not able to recognize these males as kin. Breeding females, however, appear to be choosing to more often go into groups without related males indicating that breeding females may be more selective. Overall, it seems that familiarity with male relatives might be an important factor, because females clearly avoided entering groups with familiar male kin and never were observed to stay to reproduce in a group with familiar male kin.

Female Immigration and Reproduction in relation to female kin: Implications for kin cooperation

Similar to what has been reported in other female dispersal species (Starin 1994, Watts 1994, Pope 2000, Bradley et al. 2007, Di Fiore 2009), Phayre's females end up in groups with other related females. There are several ways in which a female can end up in a group with other related female kin. For example, several females may mature to dispersal age at the same time allowing for the potential for natal cohort dispersal (Starin 1994, Parnell 2002, Stokes et al. 2003) and in fact cohort dispersal has been observed in this population (Koenig et al., unpublished). Cohort dispersal may also consist of kin and non-kin and generally can facilitate a female intitially entering into a group, where females may sometimes meet some resistance, although males may facilitate through policing female agonistic interactions and the resistence is less intense than observed in other species (e.g., mantled howler monkeys, personal observations). Nontheless, females may prevent females from entering into a group (Borries & Koenig, personal communication). Secondary dispersal of females has also been observed where, similar to gorillas, a female may reproduce in a multiple groups (Harcourt 1978, Stewart and Harcourt 1987) or even leave with an unweaned offspring. If a related female from the natal or primary group then later disperses to the same group, she may end up with either her mother or another female relative.

Such nonrandom dispersal may provide the opportunity for kin cooperation, which may enhance reproductive success as in red howlers (Crockett and Pope 1993, Pope 2000). Similarly, recent studies have suggested that such a potential for kin cooperation may not be limited to the philopatric sex (e.g., Bradley et al. 2007, but see

Langergraber et al. 2007) or to just maternal kin (e.g., Smith et al. 2003, Widdig et al. 2001). Because our results show that Phayre's leaf monkeys contain groups of related females, at first glance, female Phayre's leaf monkeys have the potential for social interactions with kin. If females disperse non-randomly into groups with related females, there is the potential for cooperative associations that could infer fitness benefits for Phayre's females (e.g., Watts 1994, Pope 2000, Silk 2002, 2007). However, in this population, there was no significant difference in conceiving an offspring whether or not other female kin were around. Thus, while kin are present, it does not appear to enhance the chances of reproducing. However, whether the rate of reproduction is enhanced in the longer term is unknown.

Female Immigration and Reproduction in relation to familiar female kin: Implications for kin competition

When it comes to competition and cooperation, previous studies have shown that kin per se might not be as important as familiarity (Bowler and Benton 2005). While the literature has been biased towards maternal affiliations, recent studies have shown evidence for cooperation in paternal siblings (Widdig et al. 2006). However, this all relies on the ability to differentiate kin versus non-kin. The concept of kin recognition in wild primates still remains largely unexplored, but might be more important than previously thought when invoking explanations of dispersal, cooperation and competition.

Although there are female kin around to potentially cooperate with we found that female relatives per se did not influence female reproduction. For example, Langergraber and colleagues (2007) found that (paternal) kin could not be recognized reliably in wild chimpanzees. Thus, contrary to what one would expect based purely on nepotistic-biased models predicting social relationships, there was actually a lack of kin-biased cooperation in wild male chimpanzees (e.g., paternal brothers) and the majority of the cases of affiliation and cooperation were among distantly related or unrelated group dyads (Langergraber et al. 2007) despite the fact that kin were around to preferentially associate with. It is possible, however, that females might bias behavior or associate preferentially with familiar female kin over non-familiar female kin. Thus, we would expect that females preferentially go to live with their kin and have the ability to recognize them as such. However, we found significantly fewer cases in which females are preferentially going into groups with familiar female kin than with unfamiliar female relatives.

More importantly, our results show that females are avoiding familiar kin and were less successful at reproducing with familiar female kin relatives in the group. In fact, because there seems to be competition for female group membership (Koenig et al. 2004, Borries et al. 2008), these results strongly suggest that kin competition is driving dispersal decisions and ultimately reproductive success in female Phayre's leaf monkeys. While indirect fitness benefits gained though cooperating with same-sexed relatives have dominated the primate literature (see overview in Silk et al. 2003, Silk 2007), these results support recent research that stresses the importance of direct fitness benefits (e.g., Langergraber et al. 2007).

However, it should be noted that despite the fact that kin competition, rather than kin cooperation, seems to influence dispersal decisions in this population, the importance of kin cooperation in for female social relationships requires further investigation. Unlike some female dispersal species (e.g., howler monkeys, Pope 2000), Phayre's females form complex female-female social relationships that may be influenced by kin associations as well as tenure, rank, and reciprocity (Larney, unpublished). Females spend a large proportion of time in affiliative (e.g., grooming, allomothering) behaviors. If and how kinship plays a role in long-term social relationships and reproductive success once a female immigrates into a group remains to be explored. In fact, group size and individual female attributes in terms of rank and nutritional condition appear to be important female strategies to further enhance reproductive success (Chapter 5).

CONCLUSIONS

Dispersal in female Phayre's leaf monkeys seems to be a condition dependent strategy. Inbreeding avoidance and group instability in addition to other potential social and ecological constraints drives female emigration in this species. Female immigration decisions are most likely weighing inbreeding avoidance and female kin relationships – particularly avoiding groups with familiar male and female kin. Infanticide avoidance, however, does not appear to factor into female dispersal decisions in this population and facilitates the transfer of females between groups with dependent offspring.

The population substructure found in this population (Chapter 3) is strongly influenced by both non-random female natal and secondary dispersal and females may test several groups throughout a lifetime. We did not find that dispersal (emigrations or immigrations) was specific to any age or reproductive status (breeding, pre-breeding and natal). Natal dispersal seems to be primarily influenced by inbreeding avoidance although there is some competition amongst females for group membership that also influence the decision to leave. Pre-breeding and breeding dispersal, on the other hand, is likely influenced by competition amongst females although these females also avoid groups with familiar male relatives. In addition, dispersal decisions appear to be guided by kin competition – more precisely females seem to avoid competition with familiar female kin by preferentially not following them into the same group to breed. Similar to what has been found in other female dispersal species (e.g., howler monkeys, Crockett and Pope 1993, Pope 1998; Milne-Edwards sifakas, Morelli et al. 2009), there is potential for contextual dispersal and this may ultimately influence a female's reproductive success. Female Phayre's were most successful at reproducing with the fewest familiar female kin present in groups.

We would like to caution studies that invoke the interpretation of non-random dispersal to only result in the potential for kin cooperation. If familiarity can be ascertained, non-random kin avoidance may also confer fitness benefits, especially for female dispersal species. It appears that altruism and other social and ecologically constraints may also factor into female reproductive success (Chapter 5). The difficulty in empirically detecting multiple causes of dispersal within populations should not be underestimated, however, because different ultimate causes often influence emigration similarly. While additional social and ecological factors likely come into play, similar to what has been suggested by Perrin and Goudet (2001), it appears that from a genetic perspective alone, inbreeding avoidance and kin competition interact to shape dispersal patterns in female Phayre's leaf monkeys.

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Figure 4.1 General focal group locations (colored) relative to neighboring groups (grey) within the study area north of the main road (green line).

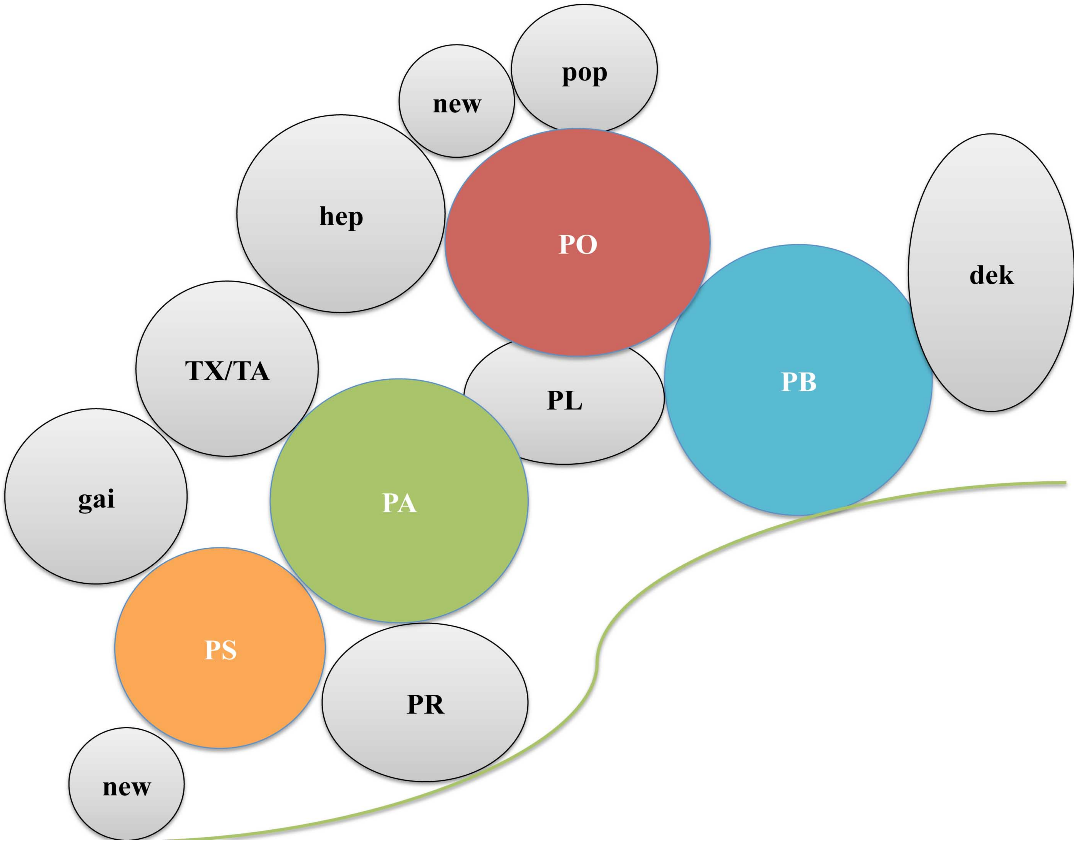

Figure 4.2 Percent of all observed female disappearances, temporary absences, and emigrations by reproductive status

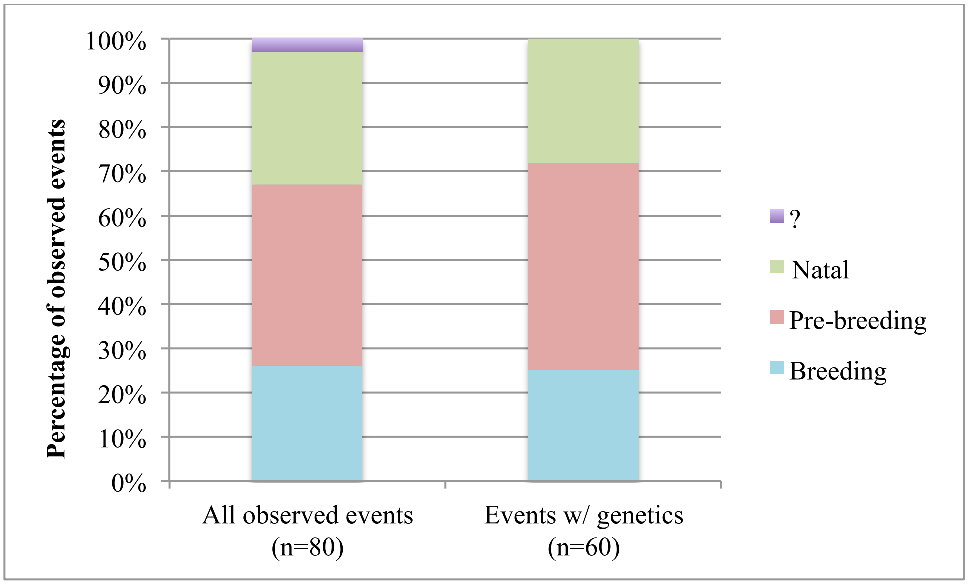

Figure 4.3 Percent of female disappearances, temporary absences, and emigration events per focal group in relation to relatedness of adult and non-adult males residing in the group prior to leaving.

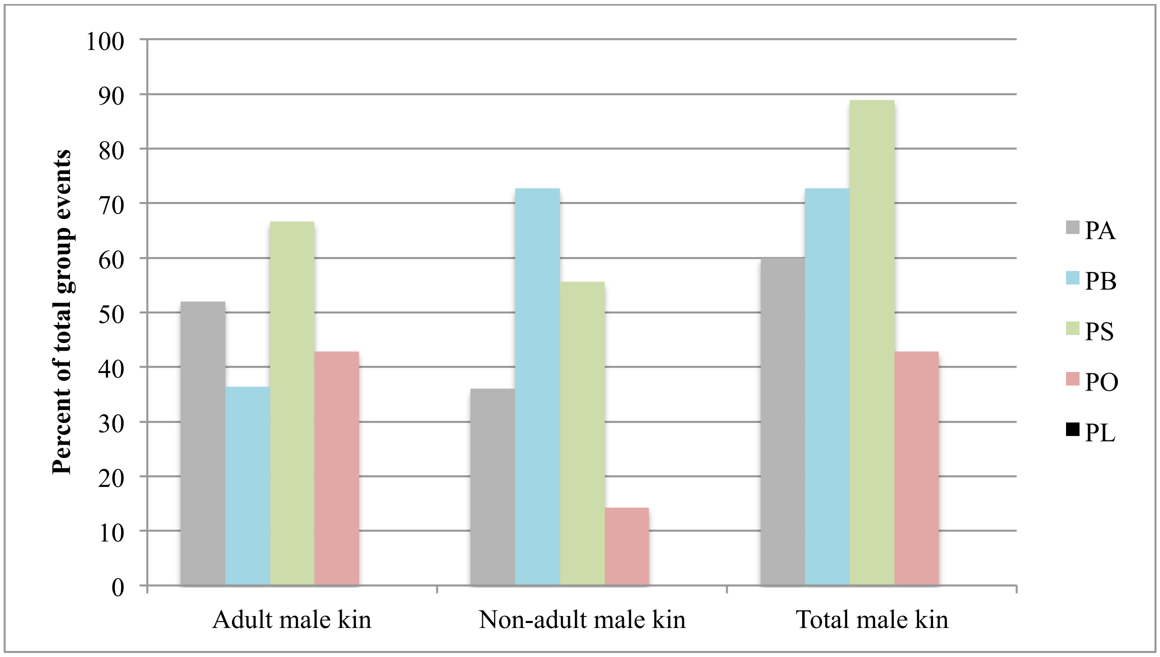

Figure 4.4 Female disappearances, temporary absences, and emigrations in relation to relatedness of females to group males prior to leaving

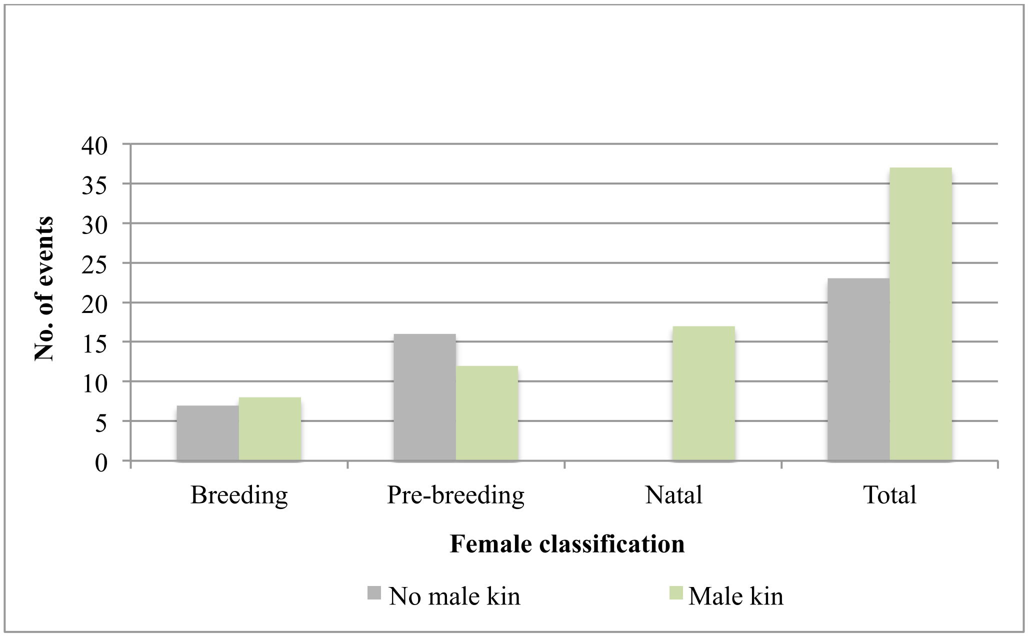

Figure 4.5 Percent of disappearances, temporary absences, and emigration events per focal group relative to female kin present

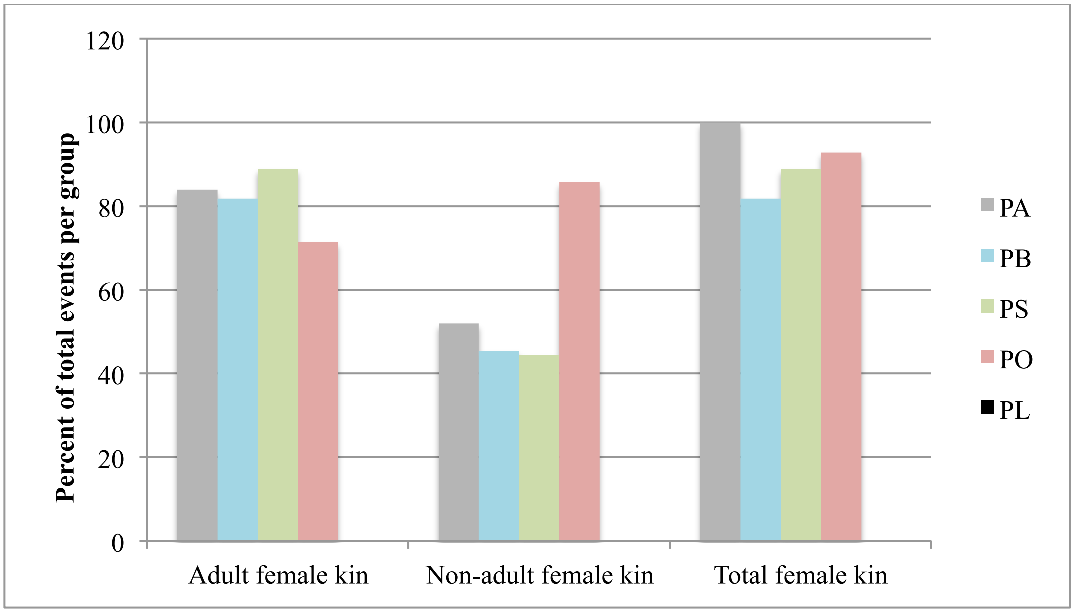

Figure 4.6 Percent of all observed female temporary absences, returns, and immigrations by reproductive status

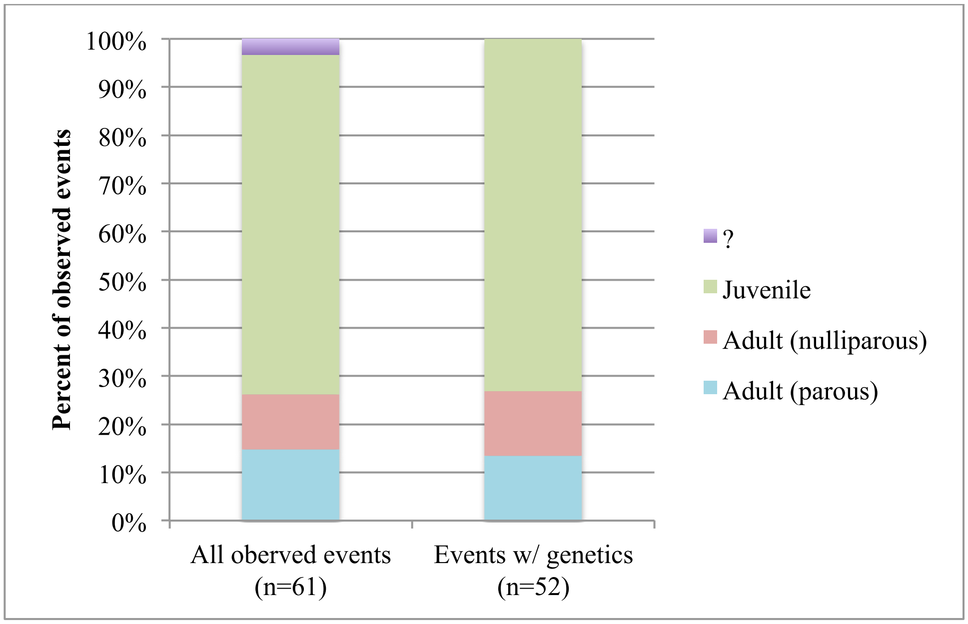

Figure 4.7 Percent of total temporary presences, returns, and immigration events per focal group relative to male kin present

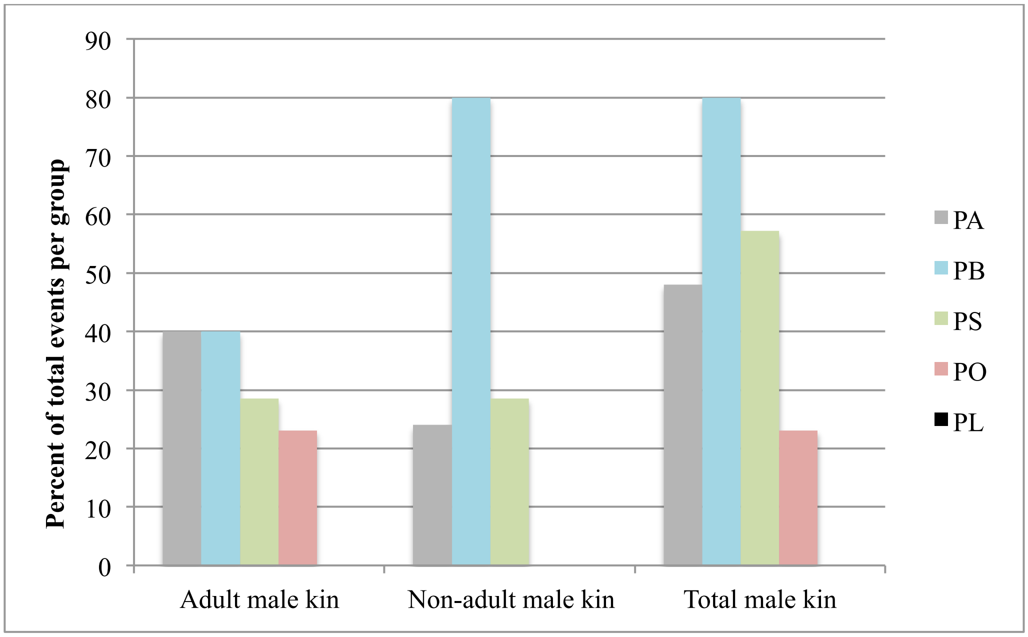

Figure 4.8 Percentage of male relatives for observed cases of temporary presences, returns, and immigrations in female Phayre's leaf monkeys

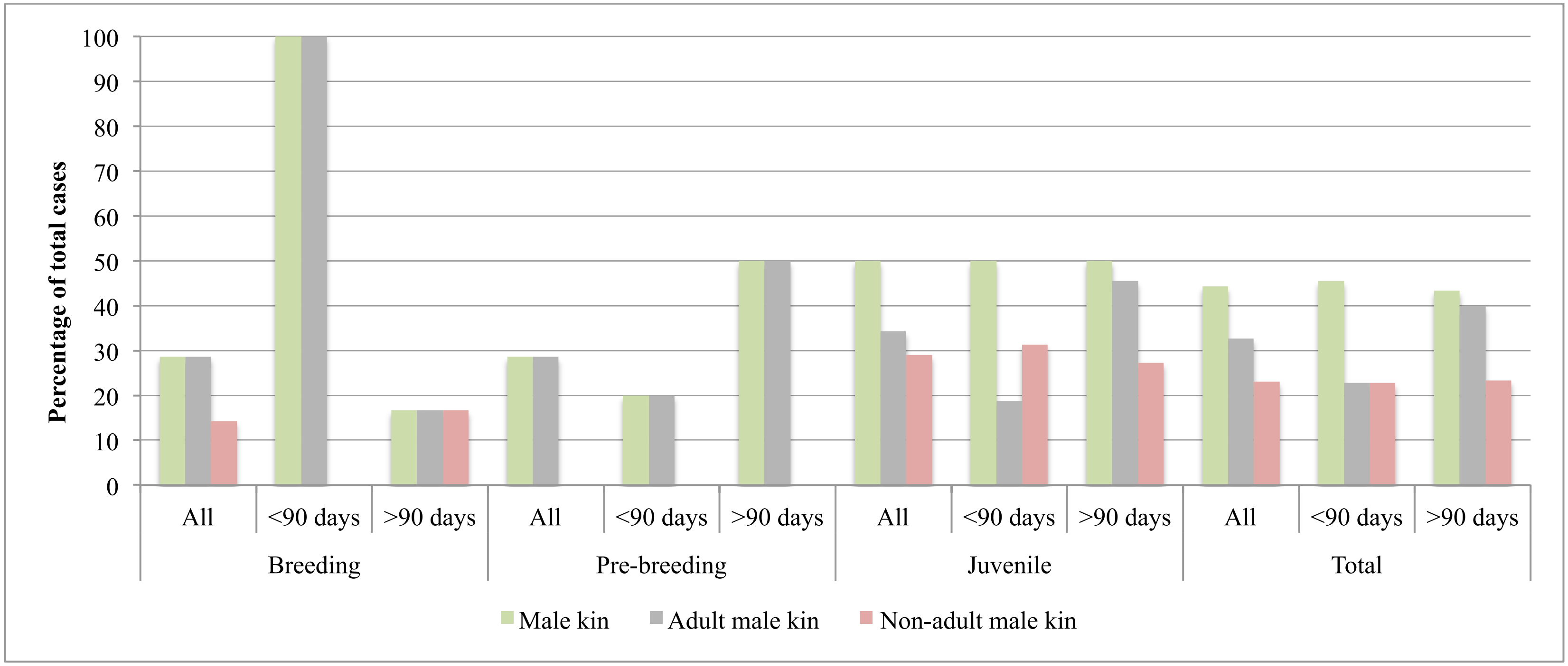

Figure 4.9 Proportion of related and unrelated males for long-term immigrant females (>90 days) that reproduced (successful) versus females that did not reproduce (unsuccessful).

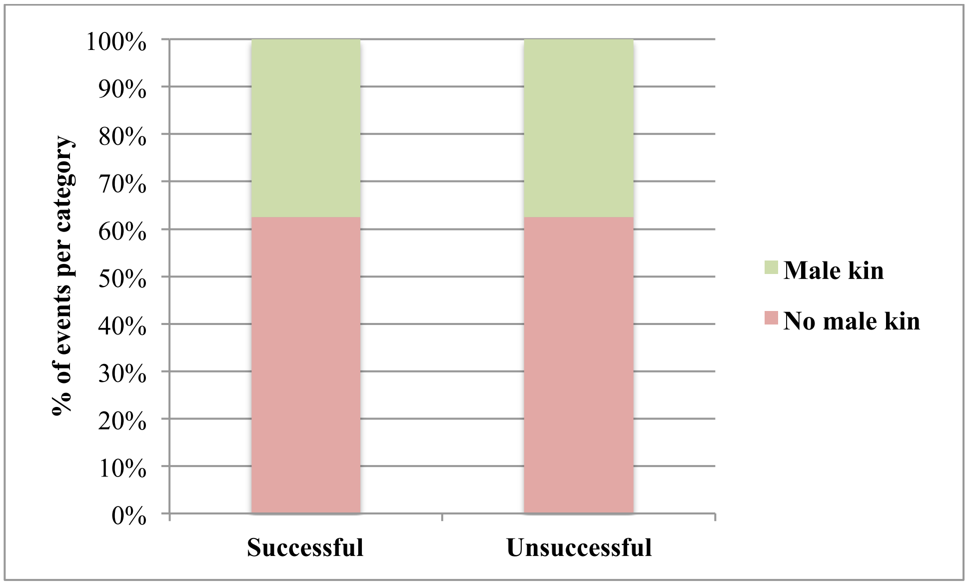

Figure 4.10 Groups female Phayre's leaf monkeys enter relative to reproductive status and the presence of female kin in groups

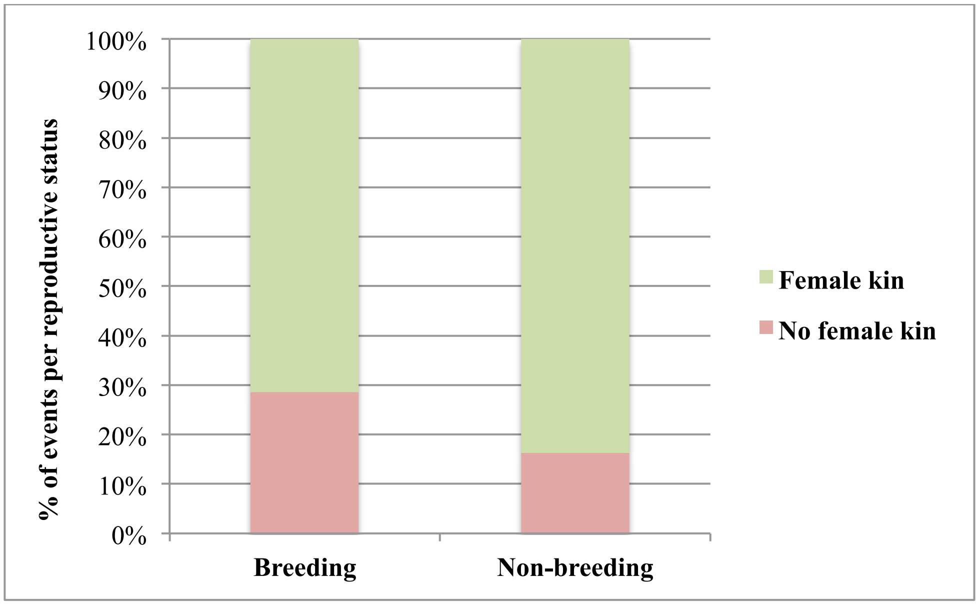

Figure 4.11 (a-b) Female reproduction following immigration based on kinship and familiarity of group females

Figure 4.11a Reproduction and overall female kinship in the group

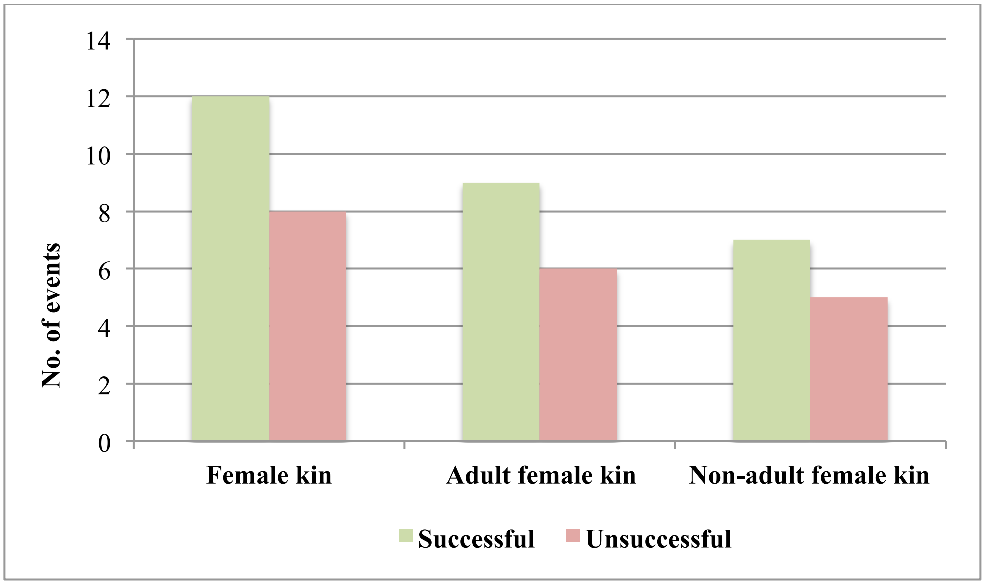

Figure 4.11b Reproduction and familiarity of female kin

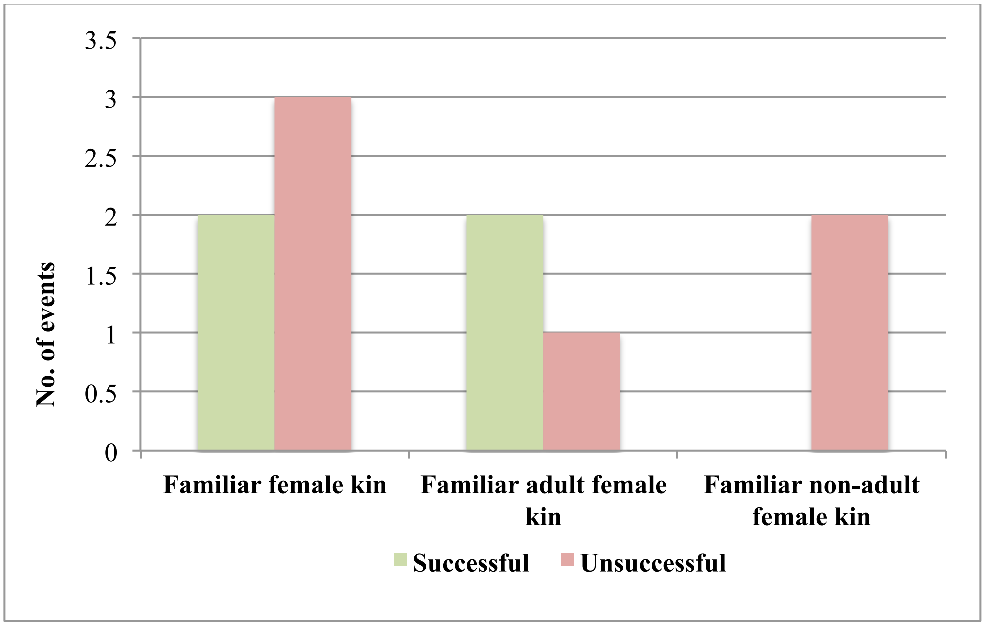

Figure 4.12 Female kinship and familiarity in relation to all cases of successful reproduction following immigration

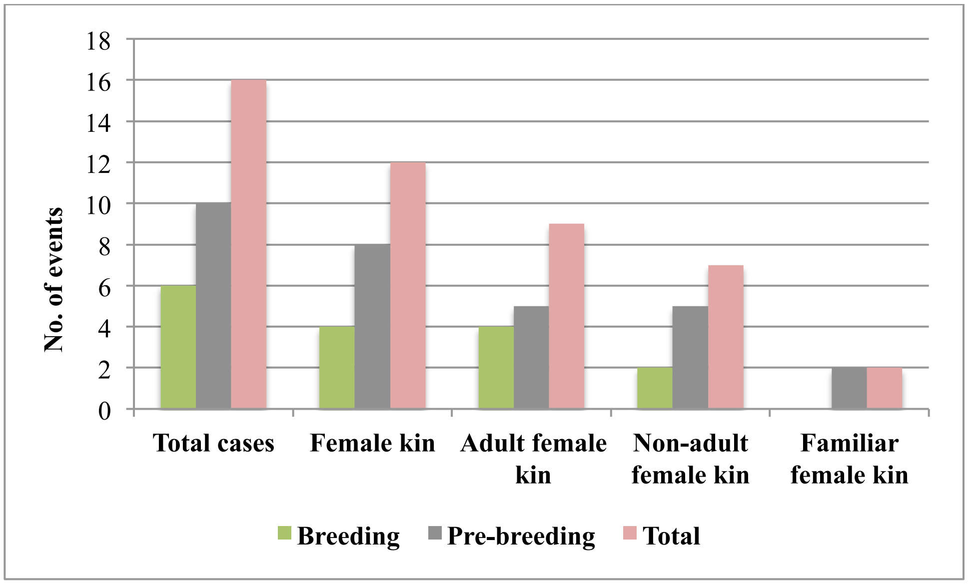

Table 4.1 Average focal group composition over 8 years of observation (January 2001 to January 2009)

Group	Data since	Adult Male	Adult Female	Subadult & Juvenile	Infant	Total
PS	Mar-02	1.2	4.3	3.1	3.4	12.1
PA	Jan-01	2.7	6.1	6.1	4.7	19.6
PO	Aug-05	2.7	7.9	3.9	6	20.5
PB	Aug-03	1.2	10.4	5.6	8.6	25.7
PL *	Dec-05	1	1	1	1	4

Note: Group means taken from Koenig & Borries (2012), except for PL (*), which was not a main focal group. Group size for PL is only given at and around the time of documented female dispersal events.

Table 4.2 Number of disappearances, temporary absences, and emigrations of female Phayre's leaf monkeys by reproductive status (2000-2009)

	Breeding	**Pre-breeding**	**Natal**	**?**	**Total**	**Rate (events/ grp-yr)**
Disappearance	12	14	14	2	42	1.8
Temporary absence [a]	1	5	2	0	8	0.3
Emigration	8	14	8	0	30	1.3
Total	21	33	24	2	80	3.4

Table 2 legend:

[a] absence of less than 90 days

Rates were calculated given an observation period of 23.24 group years

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Table 2 legend:

[a] absence of less than 90 days

Rates were calculated given an observation period of 23.24 group years

Table 4.4 Female disappearances, temporary absences, and emigrations in relation to relatedness to males in the group (up to one month before leaving)

		Breeding	**Pre-breeding**	**Natal**	**Total**
Overall sample	**Total cases**	15	28	17	60
	No male kin present	7	16	0	23
	Male kin present	8	12	17	37
Adult males	**Adult male kin present**	6	8	15	29
	All adult males are relatives	2	0	6	8
	Father present	0	0	14	14
	Son present	1	0	0	1
	Maternal brother present	0	0	1	1
Non-adult males	**Non-adult male kin present**	4	6	14	24
	Son present	2	0	0	2
	Maternal brother present	0	0	6	6
	Paternal kin present	3	0	12	15

Table 4.5 Number of female disappearances, temporary absences, and emigrations for focal groups in relation to relatedness of adult and non-adult group females. The cases in which female kin were present contained both adult and non-adult kin; thus, the sum of the last two rows does not match "female kin present".

	PA	PB	PS	PO	PL	Total
Total cases	25	11	9	14	1	60
No female kin present	0	2	1	1	1	5
Female kin present	25	9	8	13	0	55
Adult female kin present	21	9	8	11	0	49
Non-adult female kin present	13	5	4	12	0	34

Table 4.6 Number of female disappearances, temporary absences, and emigrations in relation to relatedness to females in the group (up to one month before)

	Breeding	Pre-breeding	Natal	Total
No female kin present	1	4	0	5
Female kin present	14	24	17	55
Total	15	28	17	60

Table 4.7 Number of temporary presences, returns, and immigrations in female Phayre's leaf monkeys by age and parity (2001-2009)

	Adult (parous)	Adult (nullip.)	Juv	?	Total	Rate (events/ grp-yr)
Temporary presence [a]	1	5	19	2	27	1.2
Return [b]	2	0	3	0	5	0.2
Immigration	6	2	21	0	29	1.2
Total	9	7	43	2	61	2.6

Table legend:

[a] presence of less than 90 days

[b] includes both natal and non-natal returns

Note: based on 23.25 group years

Table 4.8 Number of temporary presences, returns, and immigrations of female Phayre's leaf monkeys entering focal groups in relation to relatedness of adult and non-adult group males. The cases in which male kin were present contained both adult and non-adult kin; thus, the sum of last two rows does not match "male kin present".

	PA	PB	PS	PO	PL	Total
Total cases	25	5	7	13	2	52
No male kin present	13	1	3	10	2	29
Male kin present	12	4	4	3	0	23
Adult male kin present	10	2	2	3	0	17
Non-adult male kin present	6	4	2	0	0	12

Table 4.9 Number of temporary presences, returns, and immigrations of female Phayre's leaf monkeys in relation to resident male relatives

		Breeding			Pre-breeding			Juvenile			Total		
		<90 days	>90 days	All	<90 days	>90 days	All	<90 days	>90 days	All	<90 days	>90 days	All
Overall Sample	Total cases	1	6	7	5	2	7	16	22	38	22	30	52
	No male kin present	0	5	5	4	1	5	8	11	19	12	17	29
	Male kin present	1	1	2	1	1	2	8	11	19	10	13	23
Adult males	Adult male kin present	1	1	2	1	1	2	3	10	13	5	12	17
	Adult male kin is only adult male	0	0	0	0	0	0	0	1	1	0	1	1
	Adult male kin is father	0	0	0	0	0	0	0	2	2	0	2	2
Non-adult males	Non-adult male kin present	0	1	1	0	0	0	5	6	11	5	7	12

Table 4.10 Number of temporary presences, returns, and immigrations of female Phayre's leaf monkeys (excluding natal returns) in relation to resident male relatives

		Breeding			Pre-breeding			Total		
		<90 days	>90 days	All	<90 days	>90 days	All	<90 days	>90 days	All
Overall Sample	Total cases	1	6	7	21	22	43	22	28	50
	No male kin present	0	5	5	12	12	24	12	17	29
	Male kin present	1	1	2	9	10	19	10	11	21
Adult males	Adult male kin present	1	1	2	4	9	13	5	10	15
	Adult male kin is only adult male	0	0	0	0	1	1	0	1	1
	Adult male kin is father	0	0	0	0	0	0	0	0	0
Non-adult males	Non-adult male kin present	0	1	1	5	5	10	5	6	11

Table 4.11 Logistical regression analysis of 50 females that entered groups using reproductive status and presence/ absence of male kin as a predictor of length of female tenure in a group

Overall Model Fit	χ^2	**df**	**P-value**
	3.6654	2	0.16

Coefficients and Standard Errors	**Variable**	**Coefficient**	**SE**	**P-value**
	Breeding/ Pre-breeding	1.8386	1.1262	0.1026
	Presence/ Absence of male kin	0.0024	0.595	0.9968
	Intercept -0.0476			

Odds Ratios and 95% Confidence Intervals	**Variable**	**O.R.**	**Low**	**High**
	Breeding/ Pre-breeding	6.288	0.6916	57.1725
	Presence/ Absence of male kin	1.0024	0.3123	3.2174

Table 4.12 Female reproduction after immigration, return or temporary presence with related versus unrelated males present

	Successful	Unsuccessful	Open	Total
No male kin present	10	17	2	29
Male kin present	6	15	2	23
Total	16	32	4	52

Table 4.13 Female reproduction after immigrations, returns or temporary presences (excluding natal returns) with presence or absence of male kin

	Successful	Unsuccessful	Open	Total
No male kin present	10	17	2	29
Male kin present	6	13	2	21
Total	16	30	4	50

Table 4.14 Female reproduction after long-term immigration (> 90 days) with related versus unrelated males present

	Successful	Unsuccessful	Open	Total
No male kin present	10	5	2	17
Male kin present	6	3	2	11
Total	16	8	4	28

Table 4.15 Presence of male relatives in relation to the reproductive status of females for the 16 successful births documented during the study period

	Breeding	Pre-breeding	Total
Total cases	6	10	16
No male kin present	5	5	10
Male kin present	1	5	6
Adult male kin present	1	4	5

Table 4.16 Number of female immigration, return and temporary presence for focal groups in relation to relatedness of adult and juvenile females present. The cases in which female kin were present contained both adult and non-adult kin; thus, the sum of the last two rows does not match "female kin present".

	PA	PB	PS	PO	PL	Total
Total cases	25	5	7	13	2	52
No female kin present	3	1	2	1	2	9
Female kin present	22	4	5	12	0	43
Adult female kin present	18	4	4	10	0	36
Non-adult female kin present	10	2	3	9	0	24

Table 4.17 Number of female immigrations, returns and temporary presences for focal groups in relation to relatedness and familiarity of adult and juvenile females present.

		Breeding			Non-breeding			Total		
		<90 days	>90 days	All	<90 days	>90 days	All	<90 days	>90 days	All
Overall Sample	Total Cases	1	6	7	21	22	43	22	28	50
	No female kin present	0	2	2	4	3	7	4	5	9
	Female kin present	1	4	5	17	19	36	18	23	41
	Familiar female kin present	0	0	0	3	7	10	3	7	10
Adult Females	Adult female kin present	1	4	5	15	14	29	16	18	34
	Familiar adult female kin present	0	0	0	3	4	7	3	4	7
Non-adult females	Non-adult female kin present	0	2	2	10	10	20	10	12	22
	Familiar non-adult female kin present	0	0	0	2	2	4	2	2	4

Table 4.18 Female reproduction after long-term immigration (> 90 days) in relation to group female kinship and familiarity

		Successful	Unsuccessful	Open	Total
Overall Sample	Total cases	16	8	4	28
	No female kin present	4	0	1	5
	Females kin present	12	8	3	23
	Familiar female kin present	2	3	1	6
Adult Females	No adult female kin present	7	2	1	10
	Adult female kin present	9	6	3	18
	Familiar adult female kin present	2	1	1	4
Non-adult females	No non-adult female kin present	9	3	4	16
	Non-adult female kin present	7	5	0	12
	Familiar non-adult female kin present	0	2	0	2

Table 4.19 Female-female kinship and familiarity after immigrating into a group in relation to the 16 successful births documented during the study period

	Breeding	Pre-breeding	Total
Total cases	6	10	16
Female kin present	4	8	12
Adult female kin present	4	5	9
Non-adult female kin present	2	5	7
Familiar female kin present	0	2	2

Chapter 5

Nutritional and social maternal effects on infant development in Phayre's leaf monkeys

[Formatted for submission to Behavioral Ecology with Andreas Koenig (Department of Anthropology, Stony Brook University, Stony Brook, NY 11794-4364, USA)]

ABSTRACT

Females may influence growth, maturation, and reproduction of their offspring in various ways, but primarily through nutrition, behavioral or physiological mechanisms, or social effects such as group size or dominance rank. While some studies exist on social maternal effects in nonhuman primates in the wild, measures of maternal nutritional condition and effects on infant growth and development have been rare. This study explores the influence of group size, maternal rank, and maternal nutritional condition on infant development over the first six months of life in a population of wild Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*). To quantify infant development, we recorded the beginning, end, and duration (30 measures) in conspicuous natal coat and skin coloration of 13 infants. We assessed the physical condition of all females, including mothers, monthly (7-point scale, 19 females, 2 groups). Dominance rank was based on agonistic interactions. We found that female physical condition (both for all females and mothers only) was dependent on rank, but not on group size, and a mother's PC declined steadily after birth. There was considerable variation in infant development (e.g., total color change varied by 21 weeks) with changes in skin and coat color primarily depending on a mother's nutritional condition and group size, but less on dominance rank. Thus, in this species infants and mothers might benefit from a good maternal nutritional condition (and possibly high

rank), positively influencing speed of infant development and potentially growth, which may ultimately increase female reproductive success.

INTRODUCTION

Mammalian life histories are influenced by genetic, demographic, ecological and social factors. Individual fitness is primarily dependent on behavioral strategies pertinent for reproductive success and an individual's genetic contribution into subsequent generations through offspring survival (Clutton-Brock 1988). In turn, offspring survival depends on their phenotype, which, in addition to genetic factors, can be affected by parental non-genetic factors such as maternal effects (overviews in Kirkpatrick and Lande 1989; Bernardo 1996; Mousseau and Fox 1998; Maestripieri and Mateo 2009). Maternal effects may influence offspring fitness in various ways, primarily through nutrition, behavioral or physiological mechanisms, or social effects such as group size or dominance rank (see summary in Maestripieri and Mateo 2009).

Female mammals invest substantially in both their pre- and postnatal contribution to offspring and maternal nutritional effects are suggested to have a particularly strong influence on infant development and survival in various mammals (Côté and Festa-Bianchet 2001; Altmann and Alberts 2005; Gendreau, Côté, and Festa-Bianchet 2005; Vervaecke, Roden, and de Vries 2005). Thus, access to ecological resources is of prime importance in terms of female reproductive success in mammals (Wrangham 1980; van Schaik 1989), because levels of body fat affect ovulation, likelihood of conception, successful pregnancy and the ability to lactate (Koenig et al. 1997; McFarland 1997; Ellison 2003). In addition, it has been shown that a mother's nutritional condition influences the amount of milk yield, where females in better nutritional conditions produce a larger volume of milk compared to females in poorer condition

(Landete-Castillejos et al. 2005; Hinde, Power, and Oftedal 2009). Enhanced milk production has also been associated with accelerated infant development (Hinde 2007; Hinde, Power, and Oftedal 2009).

Maternal nutritional effects among mammals have been dominated by studies of rodents and ungulates, while mammals with long life histories, such as nonhuman primates (Charnov and Berrigan 1993; Kappeler and Pereira 2003), have been underrepresented (see summary in Maestripieri and Mateo 2009). In nonhuman primates, offspring are born in an altricial state and tend to have slow growth rates compared to other mammals (Charnov and Berrigan 1993; Kappeler and Pereira 2003). This leads to considerable dependency of infants in the first years of life and a substantial burden on the mother through lactation (Altmann 1980; Lee 1987). Although nutritional requirements vary among mammals (overview in Tardif et al. 2001), this dependency is particularly crucial for survival through the first weeks of a primate infant's life since an older infant can supplement its mother's milk with foraging and ingesting foods independently. Consequently, nonhuman primates would make very suitable subjects for the study of maternal effects. However, both measures of maternal nutritional condition and effects on infant growth and development are difficult to obtain for arboreal animals, including most primates, because the individuals are more difficult to observe.

In contrast, social maternal effects have been studied in some detail in terrestrial nonhuman primates such as baboons (Altamann 1980; Altmann and Alberts 2005). Among other aspects such as sex ratio adjustment or maternal effects on behavior (see overview in Maestripieri and Mateo 2009), it has been found that differences in dominance rank of mothers might be associated with substantial variation in offspring growth (e.g., Johnson 2003; Altmann and Alberts 2005). More generally, high rank of a mother may confer reproductive advantages in terms of shorter interbirth intervals or higher birth rates, likely indicating faster growth (Pusey, Williams, and Goodall 1997; van Noordwijk and van Schaik 1999; Altmann and Alberts 2003). However, maternal rank effects on reproductive success have not always been found (see overview in Stockley and Bro-Jørgensen 2011). In theory, females may establish dominance relationships and gain better access to food if resources can be monopolized (Janson and van Schaik 1988; overview in Koenig 2002). Under these conditions, one expects females of high rank to gain more energy (Janson 1985; Vogel 2005) and therefore be in better nutritional condition (Koenig 2000). Thus, whether dominance rank indeed confers the predicted effects on offspring growth and reproductive success depends on an actual association of rank with energy gain and maternal nutritional condition, an association that has rarely been tested, especially in arboreal primates.

However, maternal condition may not be solely rank dependent and affected by direct competition over food, but may also depend on indirect (or scramble) competition (Janson and van Schaik 1988; van Schaik 1989; Giraldeau and Caraco 2000). As group size (or density) increases, limiting food resources will be depleted faster, forcing individuals to increase foraging effort (Pyke 1984; Janson and van Schaik 1988; Chapman and Chapman 2000). As a result, individuals in large groups may be characterized by lower energy gain, which ultimately may lead to poorer maternal condition, slower growth, and reduced reproductive rates (Janson and van Schaik 1988; van Schaik 1989). While group size or density dependent effects on foraging effort or reproductive rate are well-known for nonhuman primates (van Noordwijk and van Schaik 1999; Altmann and Alberts 2005; Borries et al. 2008), the actual effects of maternal nutritional condition on infant development and growth are virtually unstudied (but see Altmann and Alberts 2005).

This study explores the influence of group size, rank, and maternal nutritional condition on infant development over the first six months of life of Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*). Phayre's leaf monkeys are arboreal group-living monkeys from Southeast Asia. In the population under study, group size effects on reproductive rates have been documented (Borries et al. 2008) and females form linear dominance hierarchies with food being the most frequently contested resource (Koenig et al. 2004a), making it likely that maternal nutritional effects are present. As in most species in the genus *Trachypithecus,* Phayre's leaf monkey infants are born with light skin and nails and a flamboyant orange natal coat (Treves 1997). Following birth, the skin and coat color change gradually to gray over a period of 5-6 months (Treves 1997). Although the color change is likely genetically pre-determined, environmental influences on the timing of color change are known and gene expression can be affected by nutrition (Caro 2005; Roulin 2009). Thus, skin and coat color change could provide measurable developmental landmarks susceptible to maternal effects. The functional significance of natal coloration has been debated elsewhere and is beyond the scope of this paper (see Treves 1997). Here we use color change as a mechanism to explore early infant development.

In the following, we present data based on a non-invasive assessment of maternal condition and a novel way to measure infant developmental landmarks in the wild. We first present results on the interrelationships between group size, rank, and maternal condition. Given that there is evidence for within-group scramble competition in this population (Borries et al. 2008) and most agonistic interactions within groups are over food (Koenig et al. 2004a), we predicted that females in smaller groups and females of higher rank should be in a better physical condition. Enhanced maternal nutritional conditions should lead to faster offspring development in the first months during infant dependency (Altmann and Alberts 2005). Consequently, we expected that infants in smaller groups, from mothers with good physical condition and of high rank to develop faster than infants in larger groups, from mothers with poor physical condition and of low rank.

MATERIALS AND METHODS

Study site and subjects

This study was conducted in Phu Khieo Wildlife Sanctuary (PKWS), Northeast Thailand (16°5’-35’ N, 101°20’-55’ E). The study site, Huai Mai Sot Yai (16°27’N, 101°38’E), consists of dry evergreen forest interspersed with patches of dry dipterocarp forest (Borries et al. 2002; Koenig and Borries in press). In addition to six other primate species, the area contains a diverse predator community including diurnal raptors, several venomous snakes including two cobra species, two python species, and 30 carnivore species including larger felids such as golden cats, clouded leopards, leopards, and tigers as well as canids such as jackals and Asian wild dogs (Grassman et al. 2005; Koenig and Borries 2012).

The population of Phayre’s leaf monkeys (*Trachypithecus phayrei crepusculus*) consists of both one and multi-male groups that vary in size from 6 to 33 individuals (Koenig and Borries 2012). Dispersal is female-biased (Borries et al. 2004) and occurs at a rate of ca. 3 female immigrations and 3 disappearances/ emigrations per group-year. Males either mature and breed in their natal group or leave to form new groups (Koenig and Borries 2012). Behavioral observations were conducted from December 2004 through May 2006 on two habituated groups (named PA and PB). Compared to the population mean of 19 individuals, including two adult males and seven adult females (Koenig and Borries in press), PA was a medium sized multi-male group that contained two adult males and a maximum of 8 adult females (Table 5.1). Four infants were born during the study period (Table 5.2). The larger group, PB, contained one adult male, 10-11 adult females and 9 infants that were born throughout observations (Tables 5.1 & 5.2). Aside from infant births, changes in group membership in both groups occurred through immigration and emigration of adult and juvenile females and maturation and disappearances (sometimes temporary) of both males and females. Throughout the study period, PB always contained several adult and juvenile individuals more than PA.

Although births can occur throughout the year in this population, most births generally occur from November to April (Borries et al. 2008). Phayre's leaf monkey infants are born with light skin and nails and a flamboyant orange natal coat (Treves 1997). Following Winkler, Vogel, and Loch (1984), we refer to this state as infant I. Change of skin and coat color to gray are completed at around 5-6 months of age (see Results). After completion of natal color change, an infant is referred to as infant II until the termination of nipple contact, at which time they are considered juvenile (at ca. 19-21 months of age; see Borries et al. 2008). Additional age estimates (adult) are based on head-body length or reproductive state with males reaching adult size at about 5-6 years of age and females giving birth to their first infant at approximately 5 years (Borries et al. 2011).

Individual identification of infant II to adult individuals was based on the shape of the crest, eye rings, muzzle, and a depigmented skin area on the lower belly as well as scars, injuries, etc. (Koenig et al. 2004b; Koenig and Borries 2012). Like many other colobines (Ross and MacLarnon 2000), female Phayre's leaf monkeys exhibit allomaternal care, i.e., females care for infants that are not their own for extended periods of time, particularly during the first months after an infant's birth. To this end, contact to a female could not be used to identify young infants (infant I) in this study. However, sex, special markers (e.g., kinks in the tail), and different color change patterns allowed for reliable individual identification of young infants non-invasively.

Physical condition of females

The nutritional status and body fatness of adult females, referred to here as physical condition (PC), was assessed in the middle of each month by visual inspection (point scale from 1-7) of every female (n = 19) with 1 representing a very poor and skinny (meager) and 7 a very healthy condition (fat) (Berman and Schwartz 1988; Koenig et al. 1997). During the assessments (conducted exclusively by E.L.), the diversity of females in stature and age was taken into account. For example, some females are generally ‘small’ or ‘large’ in stature and although a young adult female may reach adult head body length, she usually does not fill out until some years after sexual maturity. Thus, each month a female was given a score relative to her body type assessing the degree of visibility of shoulder blades, spinal column, ribs, hips, and tail bones in a standardized posture, i.e., while walking or standing quadrupedally (Koenig et al. 1997). While the assessment is subjective by nature, the method has been used previously to document changes in average PC correlating to changes in resource abundance and energy gain (Koenig 2000; Koenig and Borries 2001). In addition, individual PC appeared to affect the likelihood of conception and hence birth rate (Koenig et al. 1997; Ziegler et al. 2000; Koenig and Borries 2001). Accordingly, PC appears to be a good expression of a female's nutritional condition, which is predicted to affect infant development (see also Discussion).

We used the mean PC for each female throughout the study period for the analysis. Since all females were not present throughout the entire observation period, the sample size varies and does not always add up to 19 females in the analyses presented here. For the subset of mothers (*n*

= 13), we used two additional PC values in the analysis: the PC at birth and the mean PC of a mother from around the time of birth until her infant reached 20 weeks of age (Table 5.2). Ideally, we were also interested in comparing the PC of females from the time of conception because of the known effect of a female's nutritional condition on mammalian reproduction (Cameron 2004); however, these data were not available for all females. We selected 20 weeks because, for most infants, the color change was completed at roughly 5 months of age and these data were available for almost all mothers (for one mother it was available only up to 16 weeks due to the end of the study).

Female dominance rank

Previous observations of Phayre's leaf monkeys have shown that females display linear dominance hierarchies, in which females are ranked inversely to age (Koenig et al. 2004a). To determine female dominance ranks in this study, agonistic behavior (including aggression, submission, and displacements) was recorded using focal and *ad libitum* sampling (Martin and Bateson 2007). Agonistic data were then entered into matrices and re-ordered to fit linear hierarchies using the program MatMan (V1.1.4; Noldus Information Technology 2003). Because hierarchies were generally significantly linear or quasi-linear, we followed the I&SI method to assess ordinal dominance ranks (de Vries 1998). We used the ordering by MatMan to place females into high (H), middle (M) or low (L) rank classes within each of the two groups with rank classes set up dividing the number of females by three. Similar to what has been described for Hanuman langurs (Borries, Sommer, and Srivastava 1991), rank in female Phayre's leaf monkeys is unstable and may change over time (Koenig et al. 2004a). We assigned monthly rank classes per female and then calculated an average rank class for each female throughout the study period. In addition, we calculated an average rank class for all mothers from an infant's birth to 20 weeks of age (Table 5.2).

Infant birth and development

Most births were determined to the day or were detected within 1 or 2 days (Table 5.2). Subsequently, changes in natal coat and skin coloration were recorded weekly (until 8 weeks after birth) and bi-weekly (thereafter) to quantify infant development for all 13 infants (example in Appendix 2). The assessment was continued for individual infants up until all changes had completed.

The assessments were broken down into the following 11 categories: skin (including the face, muzzle, hands, nails on the hands, feet, nails on the feet) and coat (head, back, arms, legs, tail). Skin color change on the ears was also assessed, but this measure was discarded in the analysis, because the skin on some leaf monkeys' ears remained partially light into adulthood. The start and stop of color change were noted when possible and the duration of change was subsequently calculated. Certain variables such as the white muzzle and nails on the hands and feet received only one score (completion of change) due to difficulty pinpointing an exact start time. Thus, it was only noted when the muzzle had fully developed and when the nails on the hands and feet had changed completely gray in color. This procedure resulted in a total of 30 measures of color change. To avoid redundancy when looking at individual variables, we excluded total durations of skin and coat color change as well as total change, resulting in a total of 27 individual measures.

Statistical analysis

Statistical tests followed standard procedures as described in Sokal and Rohlf (1995) and Siegel and Castellan (1988). Descriptive statistics and inferential tests were run using STATISTICA 6.1 (StatSoft). We chose non-parametric testing, because of the small sample size and because most variables were ordinally scaled. Tests were carried out using an alpha level of 0.05. Whenever predictions were directed (see above), we calculated one-tailed test results.

To determine if group size influenced female PC, we ran a Mann-Whitney U test between all females in the medium sized group (PA) compared to the large group (PB). To control for a potential effect of seasonal variation in PC, we additionally compared the average monthly values for the females in the two groups using a Wilcoxon Signed Ranks test.

Because some of the variables that could influence infant development might potentially co-vary, we first checked for associations between age, parity, and dominance rank. As one might expect, maternal parity and age were correlated (Table 5.2; Spearman's Rank-Order correlation $R_S = 0.836$, $n = 13$, $P < 0.001$; two-tailed). Similar to our previous findings (Koenig et al. 2004a), females of the study groups displayed an age-inversed dominance hierarchy, where the youngest females had the highest dominance ranks. Because maternal parity ($R_S = 0.566$, $n = 13$, $P = 0.044$; two-tailed) and age ($R_S = 0.597$, $n = 13$, $P = 0.031$; two-tailed) were both correlated with dominance rank class, we only explored the influence of maternal rank in the analysis.

To determine associations between female rank and PC, we used Spearman's Rank-Order correlation testing average rank class of all females ($n = 15$) and average PC. For this analysis, we chose only those females that were present in the study groups throughout the entire period, excluding 4 females that were present for only a short period. We also conducted the same tests for the two groups separately. In addition to using the average values, we ran monthly correlations of rank and PC for all females within their respective groups for the entire study period.

Before assessing maternal effects, we first checked if sex of the infant influenced the speed of color change with Mann-Whitney U tests. Although there were a few significant differences (e.g., start of color change on the feet earlier for males: $U = 5.50$, $n_M = 7$, $n_F = 6$, $z_{adj} = -2.288$, $P = 0.022$; start of color change on the head earlier for males: $U = 7.00$, $n_M = 7$, $n_F = 6$, z_{adj} -2.043, $P = 0.041$) and males seemed to begin the development process slightly earlier than females, the timing of color change overall was very similar among male and female infants. Comparing all measures, the chances for a male infant to start or complete the color change before a female infant was not different from chance (one tie; $n = 15$ of 27 or 55.56%; Sign test: $z = 0.385$, $P = 0.700$). Since sex differences were not found, the following tests were run on all infants.

To determine if the color change variables were associated with mother's PC, we used a Spearman's Rank Order correlation comparing each of the 27 individual variables of infant skin and coat color change to maternal PC through the first 20 weeks of her infant's life (PC to 20 weeks). Because additional analyses using a mother's overall average PC and a mother's PC around the time of birth led to similar results, we only report the results for maternal PC through the first 20 weeks. To determine if group size influenced the speed of infant skin or coat color change, we used a Mann-Whitney U test comparing the transition from infant I to infant II in the two groups. In addition, we compared the average completion of color change for the infants in the two groups using a Wilcoxon Signed Ranks test. To test for an effect of rank class, we followed the same procedure as in the case of infant development and the mother's PC.

All analyses of color change were initially conducted in four different ways: using number of weeks, residuals from the mean and median (weeks), and ordinal ranks of the timing of color change as dependent variables. Because all of the results were similar, we only present development measured in number of weeks of an infant's life.

RESULTS

Female physical condition, group size, and rank

Monthly values of PC of all females ranged along the entire spectrum (1 (meager) to 7 (fat)) throughout the observation period (mean = 4.33, $n = 19$). Overall, we found that group size did not influence female PC. It was not higher in PA (mid-sized group) than in PB (large group) as expected over the entire 18 months (Mann-Whitney U test: $U = 24.00$, $n_1 = 5$, $n_2 = 10$, $z_{adj} = -0.123$, $P = 0.476$, one-tailed). However, month-wise comparisons of average group values of PC revealed a trend towards higher PC in the smaller group, PA (Wilcoxon Signed Ranks Test: $T = 54.50$, $z = 1.35$, $P = 0.088$, one-tailed). Contrary to the prediction, females in the larger group were in better physical condition during several of the months.

Overall, female PC was negatively correlated with average rank class (Spearman's Rank Order correlation: $R_S = -0.429$, $n = 15$, $P = 0.055$; one-tailed), i.e., highest ranking females (scored as 1) were in a better condition and lowest ranking females (scored as 3) in the worst condition. When considering the two groups separately, rank was more influential on a female's PC in the mid-sized group (PA; $R_S = -0.791$, $n = 5$, $P = 0.056$; Figure 5.1a) than in the larger group (PB; $R_S = -0.321$, $n = 10$, $P = 0.183$; Figure 5.1b). Similarly, in a month-wise comparison, we found negative correlations between rank and PC in 17 of 18 months for the mid-sized group

(PA; Binomial test: $P < 0.001$) and 11 negative correlations out of 18 for the larger group (PB; Binomial test: $P = 0.240$; Table 5.1).

Mothers' physical condition, group size, and rank

While mothers did have considerably more variation in PC throughout the entire study period, a mother's PC was never observed below a value of 3 during the first 20 weeks of her infant's life (Figure 5.2); although certain mothers (e.g., B7) fluctuated in PC much more than others (e.g., B12) following birth. On average, maternal PC steadily decreased from the birth month over the first 20 weeks of her infant's life ($R_S = –0.841$, $n = 6$, $P < 0.036$, two-tailed; Figure 5.3).

Similar to all females, we found no group differences in PC for the mothers ($U = 13.50$, $n_1 = 4$, $n_2 = 9$, $z_{adj} = –0.699$, $P = 0.252$, one-tailed), but a significant negative correlation between average rank and average PC ($R_S = –0.513$, $n = 13$, $P = 0.036$), i.e., that mothers with a high rank on average had better overall nutritional conditions than lower ranking females.

Infant development

Color change from infant I to infant II took on average 24.42 weeks (± 1.62 SE, $n = 13$). However, there was nearly a two-fold difference in variation across infants in the overall completion of color change (range: 18–39 weeks). An even stronger variation could be observed within individual measures (range: 3.5–23 weeks; Figure 5.4a and b). Among the **skin** color variables (Figure 5.4a), the face and hands were the first to change. For some infants, the face already began to start turning gray within the first week (0.5 weeks). In contrast, the feet and nails on the feet were among the last parts of the body to begin to change in color and had completely changed to gray at 8 and 9 weeks respectively. Infant **coat** color (Figure 5.4b) began to change from orange to gray at the head and the arms first, roughly at around 3 to 5 weeks of age, on average, even though it started for some infants right after birth. Head and arms were also the first coat parts that were completely changed (15 - 17 weeks). Both back and legs started to change and were completely changed in color later, while the coat on the tail started to change early, but were often the last body parts to change completely to gray. Overall, skin color change was completed sooner than completion of coat color change. More importantly, there was a large variation among infants. All measures had at least 3 weeks difference in the time it took for the skin or coat color to change and certain variables varied by as many as 13 weeks (nails on the feet) or 23 weeks (tail).

Maternal physical condition and infant development

When comparing the average PC of mothers during the first 20 weeks to the total duration of skin color change, a better maternal physical condition significantly correlated to more rapid infant skin color change ($R_S = -0.614$; $n = 13$; $P = 0.013$, one-tailed). Considering the different **skin** measures individually, 10 of the 12 variables (83.3%) were negatively correlated (Binomial test: $P = 0.019$); six of the correlations were significant (Ps < 0.05, one-tailed; Table 5.2). For example, Figure 5.5 depicts the association between maternal PC and the full development of the white muzzle of an infant ($R_S = -0.639$; $n = 13$; $P = 0.009$, one-tailed). Maternal PC was not significantly correlated to total duration of infant **coat** color change ($R_S = -0.242$; $n = 13$; $P = 0.213$, one-tailed), even though the relationship was still negative as predicted. Overall, we found that 9 out of 15 individual coat color measures (60.0%) were negatively correlated to maternal PC (Binomial test: $P = 0.304$), 4 of which were significant (Ps < 0.05, one-tailed; Table 5.2). Figure 5.6 shows an example for such a significantly negative relationship for the association of maternal PC and the duration it took for her infant's legs to turn gray (R_S = –0.622; n = 13; P = 0.012). Overall, 19 out of the total of 27 independent measures of infant color change (86%) were negatively correlated, i.e., for most measures, mothers in better nutritional condition had infants that changed skin and coat color more rapidly (Binomial test: P = 0.026).

Infant development, group size, and mother's rank

Overall, infants in the larger group (PB) completed the color change (transition to infant II) more slowly than infants in the medium-sized group (PA). On average, it took infants in the large group 26.3 weeks (± 2.0 SE, median = 25.0, range = 21–39, n = 9) to completely change both skin and coat color, compared to 20.3 weeks (± 1.31 SE, median = 19.5, range = 18–24, n = 4) in the medium-sized group (see also Borries et al. 2008). Comparing the average completion of color change of different body part variables (skin: face, hands, feet; nails: hands, feet; muzzle; coat: head, arm, leg, back, tail) for the infants of both groups, we found that infants in the larger group (PB) took significantly longer to complete color change (T = 7, z = 2.31, n = 11, P = 0.01, one-tailed; Figure 5.7).

Maternal rank during the first 20 weeks of an infant's life was not strongly associated with color change (Supplementary Data, Table 5.3). Overall, we found 15 negative and 12 positive correlations (Binomial test: P = 0.353). If anything, maternal rank appeared to influence coat development more consistently (10 negative, 5 positive correlations; Binomial test: P = 0.151) than skin color change (5 negative, 7 positive correlations; Binomial test: P = 0.387).

DISCUSSION

In addition to genetic maternal effects (e.g., Kirkpatrick and Lande 1989; Wade 1998), the importance of environmental (nutritional and social) maternal effects on offspring development is increasingly prevalent in the mammalian literature (overviews in Mousseau and Fox 1998; Maestripieri and Mateo 2009). We presented data on the variation in physical condition of female Phayre's leaf monkeys and its relation to group size and dominance rank as well as their effect on infant skin and coat color changes (aka infant development). We found that dominance rank, rather than group size, affected female physical condition. Similarly, rank appeared to influence maternal physical condition over the first 20 weeks with an infant. Using a novel method of describing natal coat and skin coloration, we found that faster skin and coat color change were associated with group size and good maternal physical condition, but to a lesser degree high dominance rank. Thus, infants and mothers might benefit from maternal effects influencing speed of infant development and potentially growth, which may ultimately affect female reproductive success.

Estimating female physical condition and the costs of lactation

We used a non-invasive assessment to determine fluctuations and variation in female physical condition. Such assessments have been used successfully for a number of primates species particularly macaques and colobines (Berman 1988; Koenig et al. 1997; Berman and Lil 2002; Lu et al. 2011). While subjective by nature, this method has been shown to have a relatively high inter-observer reliability and to correspond well to morphological measurements (Berman 1988; Berman and Schwartz 1988). Other studies indicate that variation in physical condition matched changes in overall food availability and energy intake and expenditure

(Koenig 2000; Koenig and Borries 2001). In addition, an improving physical condition was associated with a higher likelihood of conception (Koenig et al. 1997; Ziegler et al. 2000), indicating a link similar to humans between body fatness and ovarian function (McFarland 1997; Ellison 2003). Thus, while other measures such as body mass or other biomarkers (e.g., C-peptides; Sherry and Ellison 2007) are certainly more direct, these aforementioned studies support the overall usefulness of our non-invasive assessment particularly with arboreal animals, for which other measures are difficult to obtain.

For Phayre's leaf monkeys, it still remains to be seen exactly how food availability and energy gain affect physical condition. However, two lines of evidence suggest that physical condition is indeed a good indicator of nutritional and energetic status. Hormone measurements in relation to physical condition for the same animals and observation time suggest that nutritional status plays a role in the timing and likelihood of conception with females improving their condition being more likely to conceive (Lu et al. 2011). In addition, here we described that female Phayre's leaf monkeys displayed considerable variation in physical condition and some females fluctuated more so than others. When looking specifically at the window of early lactation, we found that across mothers, physical condition never fell below a value of 3, or just below average, while there was considerably more variation for these females throughout the entire study period. More importantly, the maternal physical condition decreased in value from the birth month over the first 20 weeks of an infant's life. Because births were distributed over a large range of months (from November to June), it is unlikely that a regular seasonal shortfall in resources is responsible for this decline in physical condition after birth. Instead, it suggests that females faced increased energetic demands during the first months of lactation as expected for primates and other mammals (Altmann 1980; Lee 1987; Gittleman and Thompson 1988;

Clutton-Brock, Albon, and Guinness 1989; Murray et al. 2009). As such, it seems reasonable to assume that our measure closely resembled energy reserves of females and an enhanced maternal nutritional condition may translate into higher milk production or better milk quality (Hinde, Power, and Oftedal 2009; Landete-Castillejos et al. 2010).

Female physical condition, group size, and rank

For all females over the 18 months of observation, we found considerable variation in physical condition. While group size did not have the expected effect, females of high rank, especially in the smaller group, exhibited a better nutritional condition. Many studies in mammals have shown how females living in larger groups (or at higher densities) have reduced foraging success, nutritional condition, and reproductive success (Clutton-Brock, Guinness, and Albon 1982; Janson 1988; Altmann and Alberts 2003; Focardi and Pecchioli 2005; Snaith and Chapman 2007) likely due to an increase in scramble competition with more group members or higher density (Janson 1992; Giraldeau and Caraco 2000; Parker 2000). Given that females in larger groups reproduce at a slower rate in this population (Borries et al. 2008), we expected that females in the smaller group would experience less scramble competition and this would translate into an overall better physical condition amongst females in smaller groups. However, we did not find that group size alone influenced female physical condition when comparing the mid-sized group (PA) to the larger group (PB). Overall, since both groups displayed similar variation in physical condition, one would not necessarily expect a difference based on group size alone. Why females in the mid-sized group did not have better nutritional conditions compared to the larger group is unclear. It is possible that the measure itself is too crude and the differences between a mid-size and a large group are too small to be picked up in the analysis.

However, we still found differences between rank classes. Thus, alternatively, it seems more likely that additional factors confounded the differences between groups of different size. It is possible that overall habitat differences between groups might have counterbalanced effects of scramble competition as found in ungulates and some primates (Dunbar 1987; McLoughlin et al. 2006; Harris and Chapman 2007). However, while this could explain the similar nutritional condition of females across groups, it would contrast the finding that females in larger groups reproduce at a slower pace (Borries et al. 2008). It seems more likely that the strength of scramble competition varies throughout the year masking an overall effect. Similar effects of seasonal variation of food supply and scramble competition have also been found in other leaf monkeys (Koenig 2000; Snaith and Chapman 2007). The questions as to whether and how group size affects physical condition thus awaits further analysis.

In contrast to group size, we found an overall significant effect of rank on physical condition, which was more pronounced in the smaller of the two groups. In general, if resources are contestable, dominance relationships in females often reflect the opportunity for competitive exclusion leading to an asymmetric partitioning of resources (Janson 1985; Vogel 2005). On the other hand, a good physical condition may also enable a female to achieve a higher rank. In Phayre's leaf monkeys, however, investing in and maintenance of dominance relationships seem most important for contesting over ecological resources (Koenig et al. 2004a). Thus, it is likely that agonistic interactions and high rank translated into higher energy gain as in other primates (Janson 1985; Vogel 2005) and other animals (Smith, Ruxton, and Cresswell 2001; Vervaecke, Roden, and de Vries 2005) and therefore was reflected in better nutritional condition.

Surprisingly, however, rank was more influential on a female's physical condition in the mid-sized group than in the larger group. All things being equal, one would expect that interference competition increases with group size, which should increase (not decrease) the skew in energy gain across dominance ranks (Janson and van Schaik 1988; van Schaik 1989). However, individuals may try to mitigate increasing competition through various means, e.g., non-simultaneous use of resources or increasing the group spread utilizing other resources (Larney, personal observation). This would result in a greater number of individuals in a larger group with similar foraging efficiencies (see also Janson 1990) and consequently, similar nutritional conditions. Findings from other studies of primates led to similar conclusions (van Schaik and van Noordwijk 1988; Koenig 2000) indicating that the strength of contest competition is not just a function of group size (see discussion in Koenig and Borries 2006). Overall, it appeared that rank was the most significant factor influencing the variation in female physical conditions, particularly for mothers during early lactation.

Infant development and maternal effects

Similar to what has been described for natal color change in other nonhuman primates (Treves 1997), Phayre's leaf monkey infants took approximately 6 months to change their natal skin and coat colors from flamboyant orange pelage and cream skin and nails to gray pelage, nails and skin with white muzzles. While the general length is similar to other Asian colobines (see overview in Treves 1997), we found considerable variation across infants in the overall timing of color change and more so within individual measures. The timing of natal color change ranged from at least 3 to 23 weeks (or almost 6 months) across infants. Most studies of nonhuman primate infants have not taken such fine-scale variability into account (but see Barthold, Fichtel, and Kappeler 2009).

Overall, we found that in 86% of our measures, mothers in better nutritional conditions had infants that changed color more rapidly. These results indicate that maternal nutritional condition is not only a good indicator of speed of natal color change but also a potentially useful way to measure early infant development in species with contrasting natal coloration. However, in our study, we did not test for a direct cause-effect relationship between maternal nutrition, energy transfer via lactation, and early infant development. As such, it must remain unclear whether speed of natal color change is a direct consequence of differences in the amount and quality of milk and whether this correlates with body mass of infants. However, other studies strongly support an effect of maternal body mass or fatness on growth rates of infants in both captive as well as wild populations of primates and other mammals (Johnson 2003; Altmann and Alberts 2005; Vervaecke, Roden, and de Vries 2005; Hinde, Power, and Oftedal 2009; Landete-Castillejos et al. 2010). Whether variation in speed of natal coloration change corresponds to other developmental variables (locomotion, etc.) and will have effects on juvenile growth rates and size differences will be subject to future analyses as many of the infants of this study have been subject to follow-up studies on juvenile behavior and growth.

The relationships described here have developmental implications for skin and pelage variables (Sumner and Mollon 2003; Bradley and Mundy 2008). While some previous studies indicated that pelage chromaticities do not change much with the environment or the diet (captive versus wild; Sumner and Mollon 2003), other studies point to the importance of both genetic and environmental influences for the development of coat color (Caro 2005; Bradley and Mundy 2008). In species with natal coats, it is likely that the transition from natal to adult pelage is genetically pre-determined, however, the speed of melanin-based hair color change could also reflect nutritional condition or hormone levels. If and how diet and nutrition directly influence melanin pigmentation in primates is still largely unknown (Bradley and Mundy 2008). In general, it seems clear that an adequate access to dietary nutrients can influence pigmentation in birds (Baker and Parker 1979) and mammals (Mundy et al. 1998; West and Packer 2002), which likely indicates that gene expression is sensitive to nutritional status (Roulin 2009). Thus, the strong variation in natal color change described here and its close link to maternal nutritional status suggests that the environment plays an important role in the transition from natal to adult coloration.

When looking more closely, we found that a better maternal physical condition significantly correlated with more rapid infant skin color change and this relationship was less strong, although in the similar direction, for coat color change. Interestingly, some studies suggest that skin color is more labile than fur color and is thus more likely to indicate short-term nutritional changes (Caro 2005). This finding matches our result that enhanced maternal nutritional condition might be more influential on development of skin variables compared to the coat, as maternal effects are more correlated with skin color change.

We found that group size influenced the speed of natal coat color change. Overall, infants in the medium sized group (PA) completed total color change (transition to infant II) faster than infants in the large group (PB). Similarly, infants in the larger group took significantly longer to complete color change of the different body part variables. These results match expectations based on increasing scramble competition with group size (see discussion above) and are in line with potential effects of increased scramble competition and slower growth rates on reproductive rates in this population (Borries et al. 2008). However, why group size influenced infant developmental speed and did not affect maternal physical condition is unclear.

In contrast to the direct effects of maternal nutritional condition, we did not find a strong effect of maternal rank on the speed of color change other than slightly faster coat color development compared to that of the skin. These results contrast with findings that attribute a maternal rank effect on infant development and particularly on growth rates (Johnson 2003; Altmann and Alberts 2005; Vervaecke, Roden, and de Vries 2005; Landete-Castillejos et al. 2010). While higher rank overall may be important for a female to successfully gain access to preferred resources to achieve an adequate nutritional condition for conception and gestation, rank effects may be less important during this period of early lactation. Early infant weights are often more influenced by prenatal factors (Hinde 2007). Thus, it is plausible that the correlation between higher rank and better nutrition during conception and gestation may offer females the opportunity to enhance their physical condition to acquire fat in body reserves that serve to buffer later environmental fluctuations or potential food limitations in the wild during lactation (Hinde, Power, and Oftedal 2009). Alternatively or additionally, the stronger nutritional and weaker maternal rank effect in our study could simply be the result of a more direct interrelationship between nutrition and infant development. Maternal rank is often taken as a proxy for maternal condition assuming that rank affects maternal condition and, hence, lactation and energy transfer to the infant. However, in Phayre's leaf monkeys as well as other langurs, dominance rank is not stable; females often decline in rank after birth of an infant (Borries, Sommer, and Srivastava 1991). Thus, the average rank as (necessarily) used in this study is only an approximation and maternal physical condition might be the better estimate when it comes to lactation and energy transfer. In addition, lactational characteristics of females may change with age and parity independent of rank. Studies on captive macaques showed that, independent of maternal weight, milk yield increased with parity and infants of mothers with higher parities received more energy (milk nutrients) than infants of mothers with lower parities (Hinde, Power, and Oftedal 2009). Similar effects of parity have been demonstrated in other species particularly with regard to birth weights (Fessler et al. 2005). However, as is often the case (Muruthi, Altmann, and Altmann 1991), in our sample parity was correlated with rank and age. Hence, it is difficult to disentangle these three factors and we do not know what potential effect parity (or age) might have had on energy transfer.

In conclusion, we could demonstrate environmental maternal effects (including nutritional and social effects) for infant development in Phayre's leaf monkeys. However, additional research is needed to understand the complex interrelationships between maternal condition, factors that affect this condition, energy transfer to the infants, consequences for growth rates and fitness of mothers and infants.

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Figure 5.1 Physical condition in relation to rank class for all adult females in (a.) the mid-sized group PA and (b.) the large group PB.

Figure 5.1a Physical condition in relation to rank class for all adult females in PA

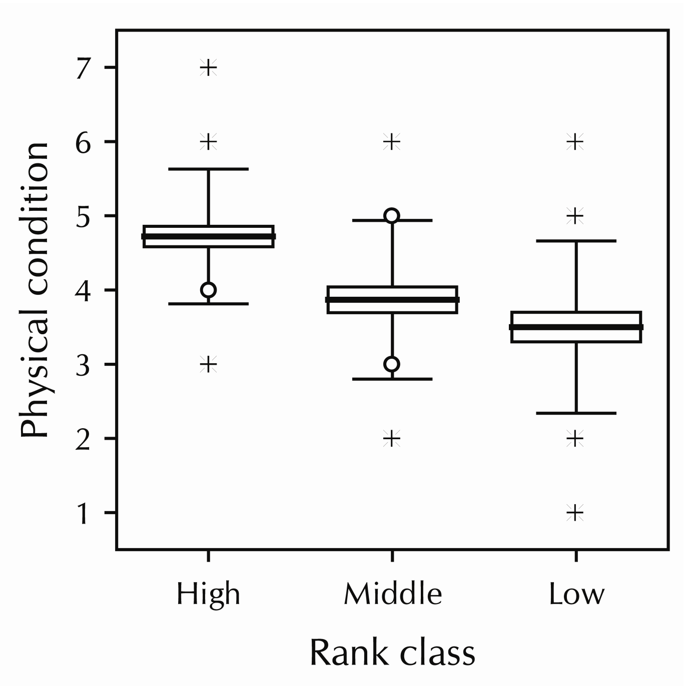

Figure 5.1b Physical condition in relation to rank class for all adult females in PB

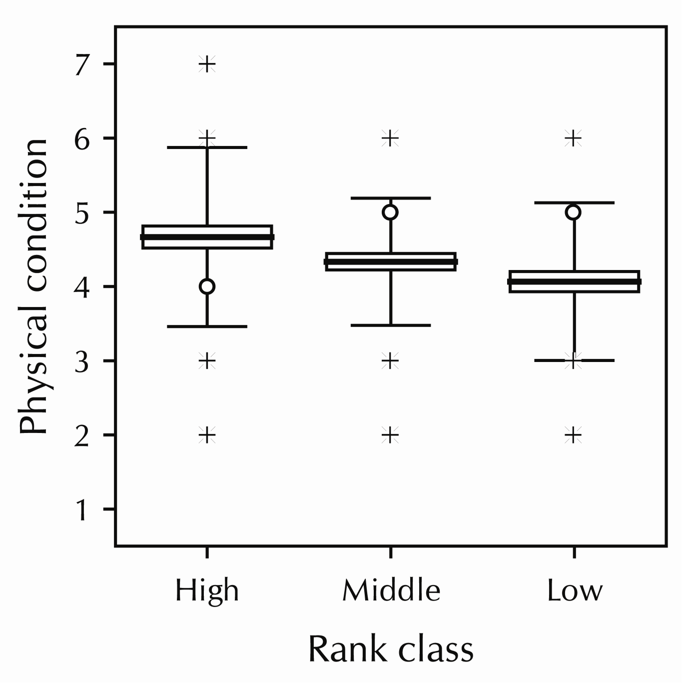

Figure 5.2 Individual variation in maternal physical condition for the first 20 weeks of an infant's life. Mean, SE (boxes), SD (whiskers), and outliers (circles) are given.

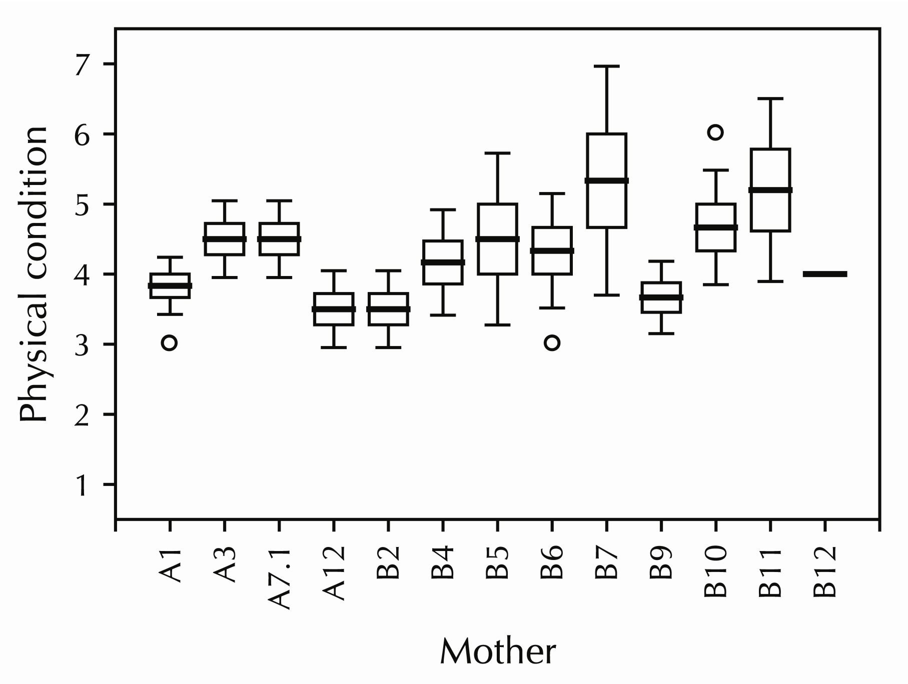

Figure 5.3 Change in average maternal physical condition from birth until 20 weeks of an infant's life. Mean, SE (boxes), SD (whiskers), outliers (circles), and extremes (crosses) are given. Regression line added for demonstration purpose only ($y = 4.94 + 0.19x$).

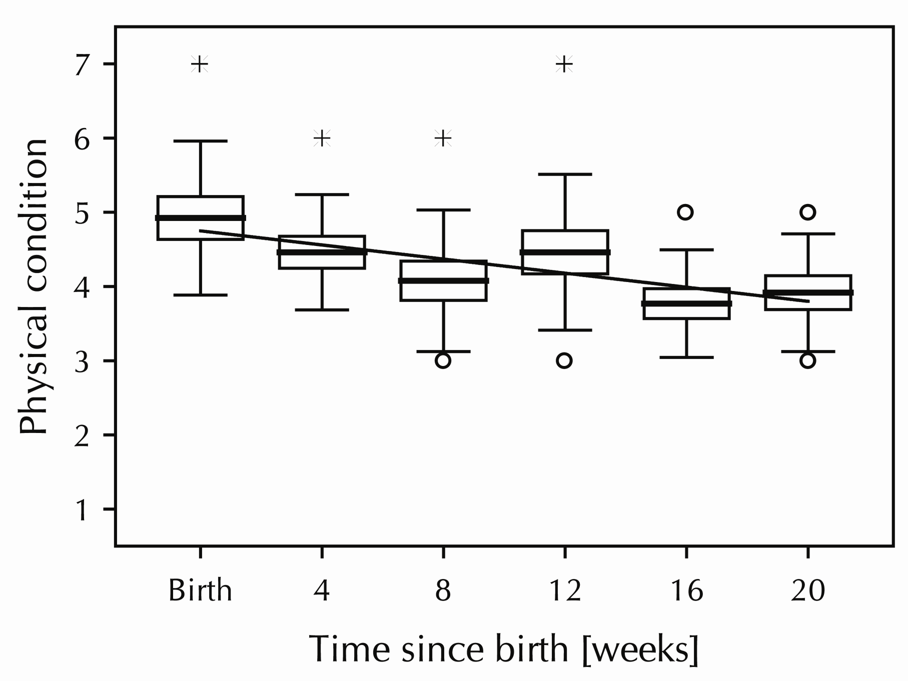

Figure 5.4 Variation in infant color change. Depicted are the start and stop of color change (a.) for the skin of face, hands, and feet as well as the time when the muzzle had developed and the color of the nails (hands, feet) had changed and (b.) for the start and stop of color change for the coat of the head, back, arms, legs and tail. Mean, SE (boxes), SD (whiskers), outliers (circles), and extremes (crosses) are given.

Figure 5.4a Start and stop of color change for the skin of face, hands, and feet as well as the time when the muzzle had developed and the color of the nails (hands, feet) changed

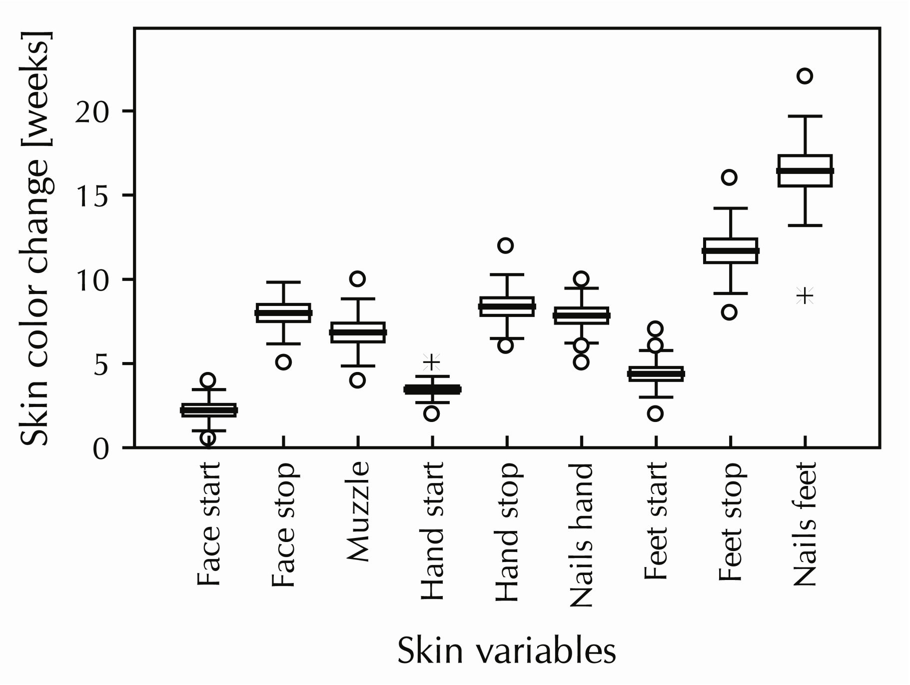

Figure 5.4b Start and stop of color change for the coat of the head, back, arms, legs and tail

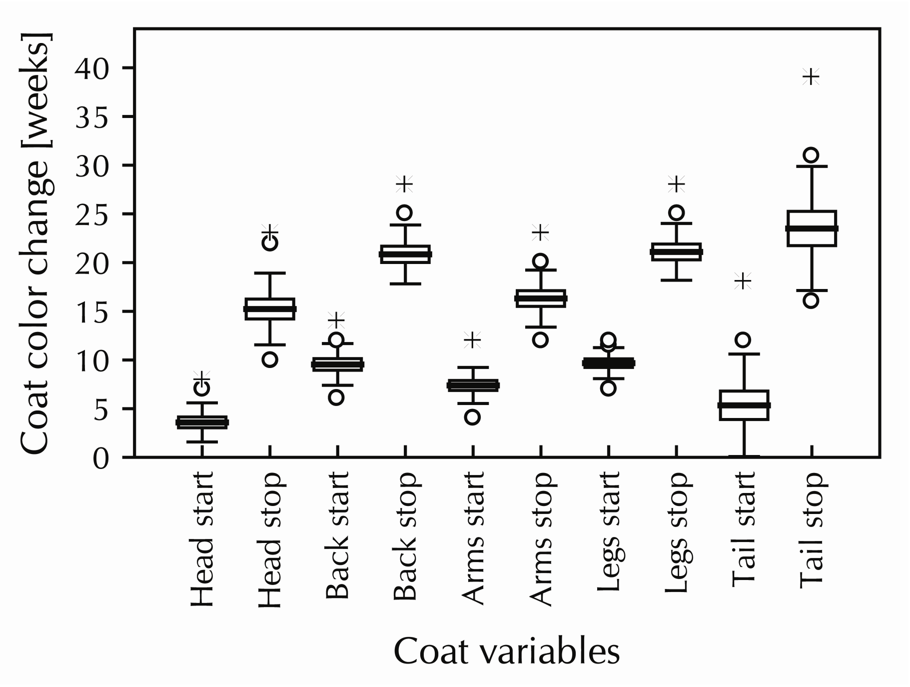

Figure 5.5 Infant muzzle development in relation to maternal physical condition (mean of physical condition from birth to 20 weeks). Regression line added for demonstration purposes only ($y = 15.15 + 1.94x$).

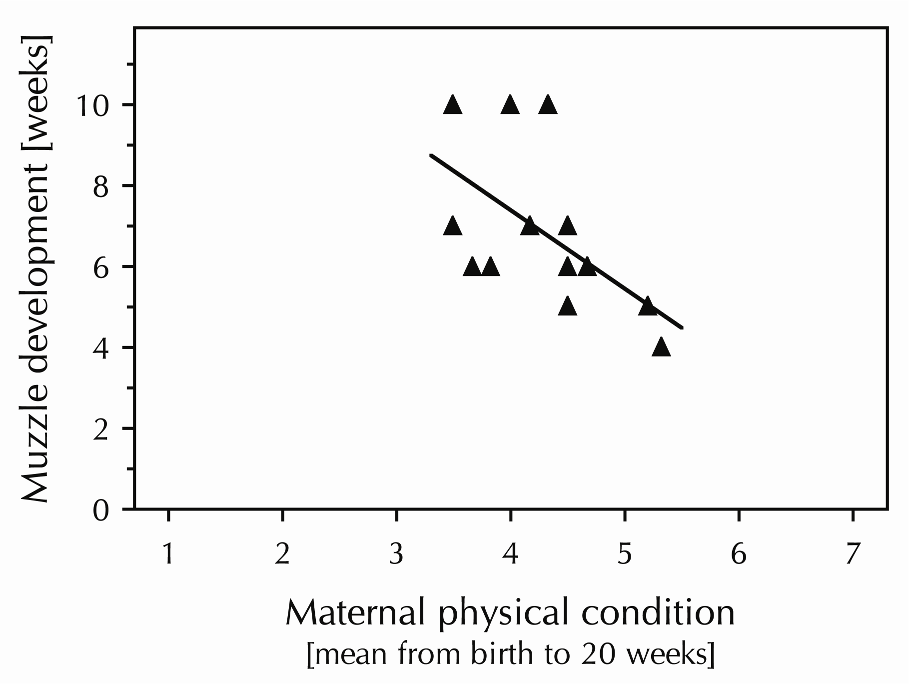

Figure 5.6 Duration of infant coat color change on the legs in relation to maternal physical condition (mean of physical condition from birth to 20 weeks). Regression line added for demonstration purposes only ($y = 24.54 + 3.06x$).

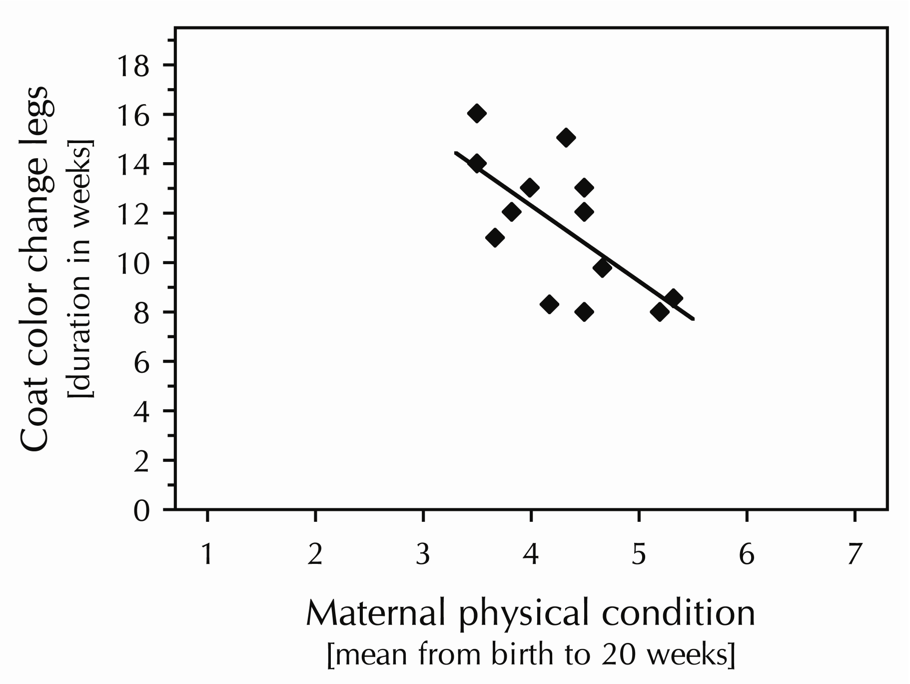

Figure 5.7 Time to completion of color change for the infants in the medium-sized group (PA, 4 infants; gray bars) and the large group (PB, 9 infants; black bars). Depicted are mean values for the infants of each group for 11 skin and coat variables.

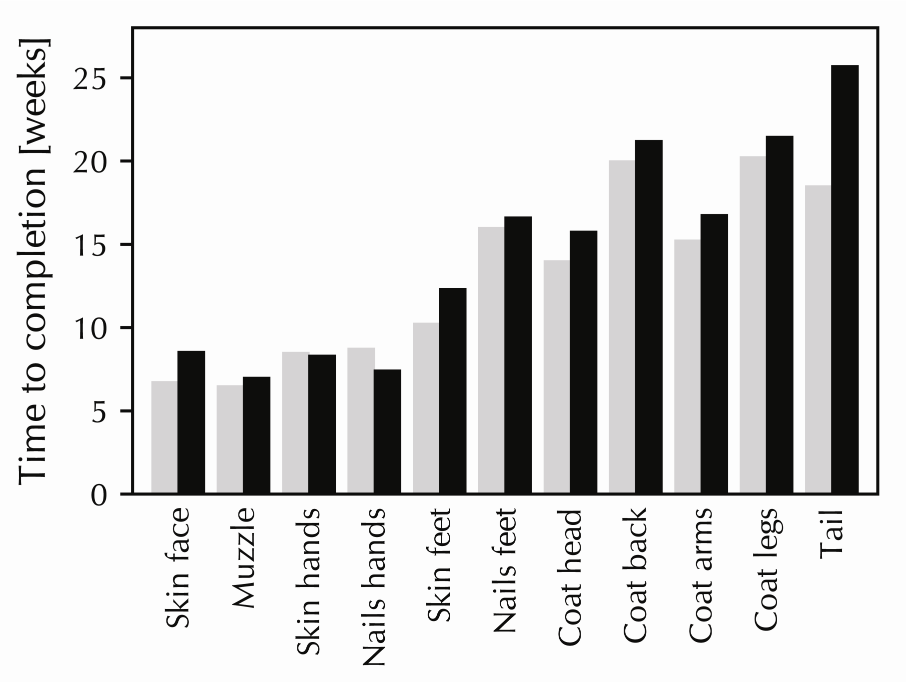

Table 5.1 Composition of the study groups over two birth seasons. The total number of individuals present over the study period is given per age and sex class. See methods for age class definitions.

	PA				**PB**			
	Oct. 2004 - Sept. 2005		Oct. 2005 - May 2006		Oct. 2004 - Sept. 2005		Oct. 2005 - May 2006	
	Male	Female	Male	Female	Male	Female	Male	Female
Adult	2	8	2	8	1	11	1	10
Juvenile	3	3	3	4	5	0	5	4
Infant II	0	1	1	2	1	3	2	3
Infant I	1	3	0	0	2	3	3	1
Total	21		20		26		29	

Table 5.2 Characteristics of females and their infants

	Females								Infants			
Group	Name	Reprod. status before birth	Age class	Mean rank class	Mean PC	Range PC	Mean PC birth to 20 weeks	Mean rank class birth to 20 weeks	Name	Sex	DOB	Age infant II [wks]
PA	A1	M	3	L	4.11	3-6	3.83	L	Am1.3	M	Mar 6, 2005*	20.0
	A3	M	3	M	3.94	2-6	4.50	M	A3.3	F	Dec 18, 2004*	19.0
	A7.1	N	1	H	5.06	4-7	4.50	H	A7.1.1	F	June 27, 2005*	18.0
	A12	N	1	H	4.17	2-6	3.50	H	A12.1	F	April 7, 2005	24.0
PB	B2	M	3	M	3.56	2-5	3.50	H	B2.2	F	Apr 18, 2005	39.0
	B4	M	3	L	4.22	3-6	4.17	M	Bm4.2	M	Dec 24, 2005*	25.0
	B5	M	2	L	4.11	2-6	4.50	M	B5.2	F	Mar 25, 2005	21.0
	B6	M	2	L	4.28	3-6	4.33	L	B6.2	F	Nov 24, 2004*	26.0
	B7	M	2	H	5.44	3-7	5.33	H	Bm7.2	M	Dec 28, 2005	29.5
	B9	P	1	M	3.89	3-5	3.67	M	Bm9.2	M	Mar 20, 2005	31.0
	B10	M	2	M	4.61	3-6	4.67	M	Bm10.2	M	Dec 28, 2005	22.0
	B11	P	1	H	5.17	3-6	5.20	H	Bm11.2	M	Feb 3, 2006*	22.0
	B12	M	2	H	4.56	3-7	4.00	H	Bm12.2	M	Feb 5, 2005	21.0

Reproductive status prior to this infant's birth: M = multiparous, P = primiparous, N = nulliparous. Age: estimated from observations since 2000 or classified by size comparisons relative to one another as (1) young (5-6 years), (2) middle (6-8 years) and (3) older (8+ years). Mean rank class: rank class averaged over the entire 18 months observation period. Mean PC: physical condition averaged for a female over the entire 18 months observation period. Range PC: lowest and highest score for physical condition during the entire 18 months observation period. * infants born within +/- 1-2 days, otherwise exact date of birth (DOB). Age infant II [wks]: age when the color change was entirely completed.

Chapter 6

The influence of genetic and social structure on reproduction in Phayre's leaf monkeys: Synthesis of findings and future directions

The goal of this dissertation was to investigate the influence of genetic and social structure on reproduction in wild Phayre's leaf monkeys. The study addressed three main goals, including: (1) to determine how groups are genetically structured and by what means, (2) to assess what influence, if any, kinship and familiarity have on female dispersal decisions and success at reproducing, and (3) to explore if nutritional and social maternal effects promote infant development following a successful reproduction. The study is among only a handful that have complementary genetic, demographic and behavioral data on a female dispersal species, only one of three such studies on dispersal (Yan 2012) or paternity (Launhardt et al. 2001) in an Asian colobine, and the only study of an Asian colobine to utilize molecular and social evidence to explore dispersal in relation to reproduction of both males and females. In the following section, I provide a synthesis of the results presented in this dissertation and suggestions of directions for future research, focusing both on methodological and theoretical issues.

Chapter 2: New markers for an Asian colobine ideal for non-invasive sampling

Molecular techniques have been widely applied to behavioral and ecological studies in recent years. The use of microsatellite markers, in particular, have proved a relatively quick and easy way to answer population and individual level questions in the wild, especially from non-invasive studies using DNA extracted from hair or feces. The utility of these markers, however, depends on finding enough markers that are variable enough to be informative for a particular species and population. Amplification issues may arise due to the presence of inhibitors (e.g., folivorous species, Bradley et al. 2001) or lack of polymorphism in a particular species (e.g., Di Fiore 2003). In addition, non-invasive samples typically provide low amounts of degraded DNA for amplification that increases the potential for allelic dropout, stuttering and subsequent production of inaccurate genotypes (Taberlet et al. 1996).

Developing primers is a useful, although a time-consuming and costly process that involves extensive time in the laboratory and manipulation of laboratory conditions. Human microsatellite primers have been increasingly utilized for many great apes and cercopithecines and prove useful to explore questions related to population structure, dispersal, kinship and parentage. However, studies utilizing microsatellite loci that display high polymorphism (e.g., over 2 alleles per locus) for other higher primates, and especially colobines, have been lacking until recent years (Di Fiore 2003, but see Sun et al. 2010, Wikberg et al. 2012). Prior to this study, only one study on parentage of Hanuman langurs (Launhardt et al. 1998, 2001) existed for Asian colobines, although the five microsatellite loci used had relatively low polymorphism and were not ideal for this study of *T. p. crepusculus*.

Nonetheless, it is becoming an increasing standard in studies of wild populations to include both demographic and behavioral data in addition to genetic data to truly answer many questions that can take years to observe in the wild, and that may never be answered or misleading due to the intricate social systems and behaviors of primates. Thus, chapter two focused on the intensive screening that was conducted for both developed and human microsatellite primers. After screening both novel and established loci I established a panel of 18 highly variable markers that genotyped consistently and accurately. Allelic diversity ranged from 5-14 alleles per locus, with expected heterozygosities ranging from 0.679-0.884. As an endangered primate species, the suite of loci can also have broader application to conservation related studies, such as monitoring genetic variability between isolated populations and genetic health (e.g., levels of inbreeding) within populations for conservation strategies. It may also serve as a useful resource for intra- and interspecific molecular studies on other Asian leaf monkeys, which are underrepresented in molecular studies but face increasing pressure due to habitat degradation and hunting for meat and medicinal value. Moreover, The application of this suite of polymorphic loci can be useful for examining population structure, dispersal, kinship and reproductive success within populations, and particularly for the population in northeastern Thailand that also has extensive behavioral and ecological studies underway.

Chapter 3: Increasing our knowledge of colobine dispersal patterns

Genetic analyses revealed that the population exhibited population substructure as indicated through Hardy Weinberg equilibrium within groups but not across the population. In addition, the population is characterized by gene flow in both sexes, although males likely disperse less frequently or at closer distances than do female conspecifics. Individuals shared low overall relatedness, although same-sexed kin were present both within and between groups. Coupling behavioral data with genetic data reveals that females natal and secondary dispersal have a strong influence on genetic structuring, although males may also contribute to gene flow by extra-group conceptions, transfer of male offspring with dispersing mothers, and by forming new groups.

Similar to what has been described for other folivorous primates (Moore 1984), female dispersal in Phayre’s leaf monkeys is quite common (Borries et al. 2008) and male dispersal has been documented as well but the extent remained unclear (Koenig & Borries 2012). However, contrary to what has been described from primarily observational studies in other female dispersal species (red colobus, Marsh 1979; hamadryas baboons, Moore 1984; gorillas, Stokes et al. 2003, Bradley et al. 2007) and colobines (Thomas' langurs, Steenbeek et al. 1999, Sterck 1997, 1998), genetic evidence suggests that both sexes are dispersing to an appreciable degree. In fact, other Asian colobines have been described as having frequent male dispersal (review in Kirkpatrick 2011, Sterck 2012) and studies incorporating both molecular and behavioral evidence in female dispersal species have found molecular support for gene flow by both sexes resulting in low levels of overall relatedness between sexes (e.g., chimpanzees, Vigilant et al. 2001, Lukas et al. 2005). Importantly, molecular analysis showed that there are both male and female kin networks both within and between groups despite dispersal (Starin 1994, Bradley et al. 2004, 2007, Di Fiore 2009). This could suggest opportunities for kin-biased behaviors and fitness benefits (Silk 2002). However, as other studies have suggested (Vigilant et al. 2001, Lukas et al. 2005, Goossens et al. 2006, Lawson Handley and Perrin 2007, Bradley et al. 2007, Harris et al. 2009, Inoue et al. 2013), it is important to consider both observational and genetic data when describing dispersal patterns. While female dispersal is indeed prevalent as indicated by both observation and genetics, it is less clear how males contribute to gene flow in this population aside from a few observations of new group formations (Koenig and Borries 2012) since observational and genetic data are somewhat contradictory.

Long-term studies of chimpanzees (*Pan troglodytes*) show that males are philopatric and females disperse, but genetic studies have found that average within-group relatedness usually does not differ between adult males and adult females (Vigilant et al. 2001, Lukas et al. 2005). Within-group relatedness for the philopatric sex may not be significantly higher than for the dispersing sex if group size is large (Lukas et al. 2005). In addition, low levels of average within group relatedness could result from non-random dispersal or if unrelated males reside in the group and multiple males sire offspring (Altmann et al. 1996). Similar to what we have found in Phayre's leaf monkeys, extra-group paternities, although rare, in combination with secondary dispersal of females with offspring in chimpanzees provide some evidence of how males may mediate gene flow despite patrilocality (Schubert et al. 2011), which can derive unexpectedly low overall variation in relatedness between sexes within a population.

However, extension of this study in several domains would be insightful. In particular, sex-linked primers (mtDNA and X- or Y-chromosomes) could provide additional insight into the current and historical dispersal pattern and how genetic structure may be influenced by sex-specific dispersal strategies (e.g. Langergraber et al. 2007, Inoue et al. 2013). In fact, the sample set was small and samples were collected form a restricted area. Additional samples from more individuals, especially within unhabituated groups, might prove insightful to ascertain further parentage analysis and also increase our understanding of how extensive kin networks may be. Increasing the collection range and georeferencing collection sites might also prove insightful to get a better understanding of the dispersal distance (Inoue et al. 2013), which can be underrepresented in sampling merely from neighboring groups. Further analysis of changes in within group relatedness in time segments (e.g., cohorts) might provide additional insight into the impact of reproductive skew on kin patterning over years (e.g., Langergraber et al. 2007) and its implications for male fitness (Bradley et al. 2005). Thus, while we have gained important insight into the genetic structure and dispersal pattern of Phayre's leaf monkeys, complementary genetic methods and larger sampling regimes (in number and locality) would be important in consider in future studies.

Chapter 4 - New insights into female dispersal decisions and reproduction

Dispersal in female Phayre's leaf monkeys seems to be a condition dependent strategy. Our results suggest that the population substructure found in this population is strongly influenced by both non-random female natal and secondary dispersal and females may test several groups throughout a lifetime. While other ecological and social variables likely influence dispersal decisions in females (Koenig et al., unpublished), we found that inbreeding avoidance and avoidance of kin competition interact to shape dispersal patterns in female Phayre's leaf monkeys from a purely genetic perspective.

We did not find that dispersal (emigrations or immigrations) was specific to any age or reproductive status (breeding, pre-breeding and natal). Although, similar to what has been described in other female dispersal species (e.g., Harcourt 1978, Pusey 1980, Mitchell et al. 1991, Glander 1992, Sterck 1997, Printes and Strier 1999, Starin 2001, Teichroeb et al. 2009, Clarke and Glander 2010), we found the majority of cases in which females left focal groups involved juvenile females. However, most juvenile cases actually involved pre-breeding, non-natal females. Natal dispersal seems to be primarily influenced by inbreeding avoidance although there is some competition amongst females for group membership that also influence the decision to leave. Pre-breeding and breeding dispersal is likely influenced by competition amongst females although these females also avoid groups with familiar male relatives. While females may enter groups containing female kin, dispersal decisions appear to be guided by kin competition – more precisely females seem to avoid competition with familiar female kin by preferentially not remaining with them in the same group to breed. As described in other female dispersal species (e.g., howler monkeys, Crockett and Pope 1993, Pope 2000; Milne-Edward's sifakas, Morelli et al. 2009), there is potential for contextual dispersal and this may ultimately influence a female's reproductive success. Our results provide new insight in that Phayre's leaf monkey females were most successful at reproducing with the fewest familiar female kin present in groups.

Similar to what has been described for other female dispersing primate species (Pusey 1980, Starin 1991, Pope 2000, Sterck 1997, Stokes et al. 2003, Bradley et al. 2007, Morelli et al. 2009, Di Fiore 2009, Teichroeb et al. 2009, Lukas and Clutton-Brock 2011, Clutton-Brock and Lukas 2012), our results show that inbreeding avoidance is an important factor for both natal and secondary dispersal in female Phayre's leaf monkeys. However, almost a quarter of time a female left a group unrelated males were present, indicating that inbreeding may not be the only reason for non-natal transfers and additional social contexts involving males may also influence if and when a female decides to leave such as rank changes or groups disbanding (Stokes et al. 2003, Di Fiore 2009). From our current knowledge, infanticide avoidance does not appear to influence female dispersal decisions. In fact, females sometimes transferred between groups with dependent offspring similar to some other colobines (e.g., *T. johnii*, Poirier 1970; *P. siamensis*, Bennett 1983; *N. larvatus*, Bennett and Sebastian 1988), but unlike what has been observed in other species that found female transfer closely linked to infanticide avoidance (e.g., red howler monkeys, Crocket and Pope 1993; Thomas langurs, Sterck 1997; western lowland gorillas, Stokes et al. 2003; Milne-Edward's sifaka, Morelli et al. 2009, ursine colobus, Teichroeb et al. 2009), it seems that infanticide avoidance may not be an influential factor in dispersal decisions of Phayre's females. While much of our knowledge on infanticide in colobines has come from studies on Hanuman langurs (e.g., Mohnot 1971, Hrdy 1974, Borries 1997), infanticide by males has also been reported in other colobine species (e.g., *Colobus guereza*, Onderdonk 2000; *C. vellerosus*, Teichroeb and Sicotte 2008, *Nasalis larvatus*, Agoramoorthy and Hsu 2005;

Presbytis thomasi, Steenbeck 2000; *Rhinopithecus bieti*, Xiang and Greuter 2007; *Trachypithecus leucocephalus*, Zhao et al. 2011). However, despite eight years of continuous observations (representing more than 23 group years) infanticide by males has never been observed in the study population. At present, we can only speculate about the possible causes: For reasons yet to be disclosed unfamiliar males very rarely immigrate into existing groups, which eliminates the classic scenario for infanticide by males in primates Hrdy 1979. Furthermore, dispersal by females occurs frequently suggesting it to not be very costly. Consequently, if females would lose an infant to infanticide, they might subsequently disperse leaving infanticidal males with no females to breed with. In addition, as shown in Chapter 3, males in multimale groups may be relatives, which should reduce the likelihood of infanticide. Furthermore, in contrast to Hanuman langurs, Phayre's leaf monkey males interact regularly with even very young infants, which could be interpreted as a signal to females of their "friendly intentions".

Nonetheless, female kin associations have been shown to improve female reproductive success, infant survival, longevity and, ultimately, fitness (Silk 2002, Silk et al. 2003, Silk et al. 2009, Silk et al. 2010), even among the dispersing sex (Crockett and Pope 1993, Pope 1990, 2000). Despite dispersal, female kin are present within groups in this population, which has also been described in other female dispersing species (Starin 1994, Watts 1990, 1994, Pope 2000, Bradley et al. 2007, Di Fiore 2009). In fact, non-random dispersal through transferring in cohorts or following kin to groups (Starin 1994, Parnell 2002, Stokes et al. 2003) and reproducing in multiple groups through secondary dispersal (Harcourt 1978, Stewart & Harcourt 1987) likely results in same-sexed kin across groups in this population. However, contrary to what would be expected if kin selection were driving females to stay and cooperative with kin, we found that in

92% of cases, females left groups despite having female kin present, including both natal but more surprisingly non-natal females as well. Nonetheless, if females disperse non-randomly into groups with related females, there is the potential for cooperative associations that could infer fitness benefits for Phayre's females (e.g., Watts 1994, Pope 2000, Silk 2002, 2007). However, we did not find a significant difference in conceiving an offspring to term whether or not other female kin were around. Thus, the presence of female kin does not appear to enhance the chances of reproducing, although benefits via kin-selection on long-term reproductive rates remains unknown. However, when it comes to competition and cooperation, previous studies have shown that kin per se might not be as important as familiarity (Bowler & Benton 2005). Our results provide some of the first evidence that females are actually avoiding familiar kin and were less successful at reproducing with familiar female kin relatives in the group. In fact, because there seems to be competition for female group membership (Koenig et al. 2004, Borries et al. 2008), these results strongly suggest that kin competition is driving dispersal decisions and ultimately reproductive success in female Phayre's leaf monkeys. While indirect fitness benefits gained though cooperating with same-sexed relatives have dominated the primate literature (see overview in Silk et al. 2003, Silk 2007), these results support recent research that stresses the importance of direct fitness benefits (e.g., Langergraber et al. 2007).

From other observations it is known that, in addition to inbreeding avoidance, several social influences likely influence a female's decision to leave. In particular, it appears that large group size (Borries et al. 2008), agonism by other females, male turnovers, and unsuccessful reproduction may influence when a female may leave (Koenig et al., unpublished). Such social and ecological costs may outweigh potential the benefits of female kin associations within the group (Isbell and van Vuren 1996, Bradley et al. 2007, Teichroeb et al. 2009, but see Mitchell et al. 1991). This together with the dispersal away female from relatives seems to indicate a strategy of avoidance of kin competition. However, it should be noted that despite the fact that kin competition rather than kin cooperation seems to be important for dispersal decisions in this population, the importance of kin cooperation in for female social relationships requires further investigation. Unlike some female dispersal species (e.g., howler monkeys, etc.), Phayre's females form complex female-female social relationships that may be influenced by kin associations as well as tenure, rank, and reciprocity (Larney & Koenig, unpublished). Females spend a large proportion of time in affiliative (e.g., grooming, allomothering) behaviors. Although having same-sexed kin in a social group does not necessarily translate into a kin-bias in affiliative or cooperative behaviors (e.g., Seyfarth and Cheney 1984, Muroyama 1994, Henzi and Barrett 1999, Silk et al. 1999, Barrett et al. 2000, Mitani et al. 2002, Boesch et al. 2006, Langergraber et al. 2007), if and how kinship plays a role in long-term social relationships and reproductive success once a female immigrates into a group remains to be explored. In addition, group size and individual female attributes in terms of rank and nutritional condition appear to be important female strategies to further enhance reproductive success (Chapter 5). Nonetheless, our results suggest that if familiarity can be ascertained, while kin-biased affiliative and cooperative behaviors may have important implications on female social relationships and reproductive success, kin avoidance may also confer fitness benefits, especially for female dispersal species.

Chapter 5 - Maternal effects on infant development: Contributions from a colorful colobine

Given the results of Chapter 3, it would appear that there were potential for female kin networks that could potentially offer dispersing Phayre's females the opportunity for kin-biased behaviors that have been known to translate into improving female fitness in other species (Silk et al. 2003). However, results of Chapter 4 showed that female kin are actively avoiding one another and it is likely that other individual and social attributes have a stronger influence than nepotism in contributing to some aspects of a females reproductive success in Phayre's leaf monkeys. In fact, females may influence growth, maturation, and reproduction of their offspring in various ways, but primarily through nutrition, behavioral or physiological mechanisms, or social effects such as group size or dominance rank. In addition to genetic maternal effects (e.g., Kirkpatrick and Lande 1989, Wade 1998), the importance of environmental (nutritional and social) maternal effects on offspring development is increasingly prevalent in the mammalian literature (overviews in Mousseau and Fox 1998; Maestripieri and Mateo 2009).

Female mammals invest substantially in both their pre- and postnatal contribution to offspring and maternal nutritional effects are suggested to have a particularly strong influence on infant development and survival in various mammals (Côté and Festa-Bianchet 2001, Altmann and Alberts 2005, Gendreau et al. 2005, Vervaecke et al. 2005). Thus, access to resources is of prime importance in terms of female reproductive success in mammals (Wrangham 1980, van Schaik 1989). The period of maternal dependency by altricial primate infants is particularly crucial for survival through the first weeks of life and ultimately influences both the mother and infant's fitness (Charnov and Berrigan 1993, Kappeler and Pereira 2003). However, measures of maternal nutritional condition and effects on infant growth and development are difficult to obtain, especially for arboreal primates.

Studies on social maternal effects in nonhuman primates in the wild (Altmann 1980, Altmann and Alberts 2005, overview in Maestripieri and Mateo 2009), also indicate how the influence of dominance rank and group size may influence maternal condition, translating into variation in offspring survival and growth. In fact, high maternal rank may confer reproductive advantages in terms of shorter interbirth intervals or higher birth rates, likely indicating faster growth (Pusey et al. 1997; van Noordwijk and van Schaik 1999, Altmann and Alberts 2003, but see overview in Stockley and Bro-Jørgensen 2011). However, maternal condition may not be solely rank dependent and affected by direct competition over food, but may also depend on indirect (or scramble) competition (Janson and van Schaik 1988, van Schaik 1989, Giraldeau and Caraco 2000). Due to increased foraging effort (Pyke 1984, Janson and van Schaik 1988, Chapman and Chapman 2000), individuals in larger groups may be characterized by lower energy gain, which ultimately may lead to poorer maternal condition, slower growth, and reduced reproductive rates (Janson and van Schaik 1988, van Schaik 1989). While group size or density dependent effects on foraging effort or reproductive rate are well known for nonhuman primates (van Noordwijk and van Schaik 1999, Altmann and Alberts 2005, Borries et al. 2008), the actual effects of maternal nutritional condition on infant development and growth are virtually unstudied (but see Altmann and Alberts 2005).

We presented data on the variation in physical condition of female Phayre's leaf monkeys and its relation to group size and dominance rank as well as their effect on infant skin and coat color changes (aka infant development). While it still remains to be seen exactly how food availability and energy gain affect nutritional condition, our measure of physical condition appears to be a good indicator of nutritional and energetic status. Hormone measurements in relation to physical condition for the same animals and observation time suggest that nutritional status plays a role in the timing and likelihood of conception with females improving their condition being more likely to conceive (Lu et al. 2011). In addition, we found considerable variation in physical condition across females, with some females fluctuating more than others at different times of the year that is unlikely a result of an overall shortfall of resources.

We found that dominance rank, rather than group size, affected female physical condition. Similarly, rank appeared to influence maternal physical condition during early lactation, despite an overall decline across females. Surprisingly, however, rank was more influential on a female's physical condition in the mid-sized group than in the larger group. We suggest that individuals may try to mitigate increasing competition through various means, e.g., non-simultaneous use of resources or increasing the group spread utilizing other resources (Larney, personal observation), which could result in a greater number of individuals in a larger group with similar foraging efficiencies (see also Janson 1990) and consequently, similar nutritional conditions. Other primate studies have led to similar conclusions (van Schaik and van Noordwijk 1988, Koenig 2000) indicating that the strength of contest competition may not necessarily be a function of group size (see discussion in Koenig and Borries 2006).

However, given that females in larger groups reproduce at a slower rate in this population (Borries et al. 2008), we expected that females in the smaller group would experience less scramble competition and this would translate into an overall better physical condition amongst females in smaller groups. However, we did not find that group size alone influenced female physical condition when comparing the mid-sized group to the larger group. Overall, since both groups displayed similar variation in physical condition, one would not necessarily expect a difference based on group size alone. Why females in the mid-sized group did not have better nutritional conditions compared to the larger group is unclear. It is possible that the measure itself is too crude and the differences between a mid-size and a large group are too small to be picked up in the analysis. However, we still found differences between rank classes. Thus, it seems more likely that additional factors confounded the differences between groups of different size and that overall habitat differences between groups might have counterbalanced effects of scramble competition as found in ungulates and some primates (Dunbar 1987, McLoughlin et al. 2006, Harris and Chapman 2007). However, while this could explain the similar nutritional condition of females across groups, it would contrast the finding that females in larger groups reproduce at a slower pace (Borries et al. 2008). It seems more likely that the strength of scramble competition varies throughout the year masking an overall effect. Similar effects of seasonal variation of food supply and scramble competition have also been found in other leaf monkeys (Koenig 2000, Snaith and Chapman 2007). Thus, further analysis should explore whether and how group size affects physical condition in this population.

We documented early infant development using a novel method of describing natal coat and skin coloration. While the general length of natal color change is similar to other Asian colobines (see overview in Treves 1997), our results show considerable variation across infants. In addition, we found that in 86% of our measures, mothers in better nutritional conditions had infants that changed color more rapidly and suggest that maternal nutritional condition is not only a good indicator of speed of natal color change but also a potentially useful way to measure early infant development in species with contrasting natal coloration. In addition, we found that nutritional condition was more influential on development of skin variables, which may be more labile than fur color and is thus more likely to indicate short-term nutritional changes (Caro 2005).

Our results on group size effects on speed of development match expectations based on increasing scramble competition with group size (see discussion above) and are in line with potential effects of increased scramble competition and slower growth rates on reproductive rates in this population (Borries et al. 2008). However, why group size influenced infant developmental speed and did not affect maternal physical condition is unclear.

In addition, we did not find a strong effect of maternal rank on the speed of color change in contrast to findings that attribute a maternal rank effect on infant development and particularly on growth rates (Johnson 2003, Altmann and Alberts 2005, Vervaecke et al. 2005, Landete-Castillejos et al. 2010). While an overall higher rank may be important for a female to successfully gain access to preferred resources to achieve an adequate nutritional condition for conception and gestation (Hinde 2007), rank effects may be less important during this period of early lactation and/ or the result of a more direct interrelationship between nutrition and infant development due to our measure of average rank. In Phayre's leaf monkeys as well as other langurs, dominance rank is not stable and females often decline in rank after birth of an infant (Borries et al. 1991) and lactational characteristics of females may change with age and parity independent of rank (Hinde et al. 2009). However, as is often the case (Muruthi et al. 1991), parity was correlated with rank and age in our sample and thus, it is difficult to know what potential effect parity (or age) might have had on energy transfer. Thus, maternal physical condition might be the better estimate when it comes to lactation and energy transfer in this species.

Our results indicate that Phayre's infants and mothers may benefit from a good maternal nutritional condition (and possibly high rank), positively influencing speed of infant development and potentially growth, which may ultimately increase female reproductive success. We present some of the first results on environmental maternal effects (including nutritional and social effects) on infant development in the wild, especially by incorporating measures of maternal nutritional condition and early infant development using natal color change as a developmental landmark. This methodology could be widely applicable to assess nutritional variation in the wild and especially for other primate species with natal coat coloration. However, additional research is needed to understand the complex interrelationships between maternal condition, factors that affect this condition, energy transfer to the infants, consequences for growth rates and fitness of mothers and infants. Firstly, while color change appears to be a good indicator of early development, it is still unknown exactly if and how diet and nutrition directly influence melanin pigmentation in primates (Bradley and Mundy 2008). However, other studies strongly support an effect of maternal body mass or fatness on growth rates of infants in both captive as well as wild populations of primates and other mammals (Johnson 2003, Altmann and Alberts 2005, Vervaecke et al. 2005, Hinde et al. 2009; Landete-Castillejos et al. 2010) and using natal color changes as a developmental landmark could have important contributions to exploring these relationships in the wild. Similarly, whether variation in speed of natal coloration change corresponds to other developmental variables (locomotion, etc.) and will have effects on juvenile growth rates and size differences are still under investigation (Ossi and Koenig, unpublished).

Conclusions

Overall, this study provided the first results on molecular evidence of dispersal and reproductive patterns and maternal effects on infant development in Phayre's leaf monkeys. The establishment of a suite of polymorphic autosomal loci resulting from non-invasive sampling is an important tool for future molecular and behavioral studies as well as conservation management strategies for Asian colobines. Molecular results in this study provide an important contribution to the dispersal database exploring population structure and factors influencing female dispersal decisions in a wild colobine. In addition, it is the first study in a wild primate population to couple both molecular and long-term demographic data to explore the influence of kinship and familiarity on female immigration decisions and success at reproducing. This study also provides some of the first evidence of maternal effects on infant development in the wild, especially by incorporating measures of maternal nutritional condition and early infant development using natal color change as a developmental landmark. This methodology could be widely applicable to assess nutritional variation in the wild and especially for other primate species with natal coat coloration. Furthermore, results found in the present study provide an important comparative database for future studies to evaluate population and species differences in dispersal patterns, social behavior, reproductive success, and ultimately fitness, in female dispersal species and across primates.

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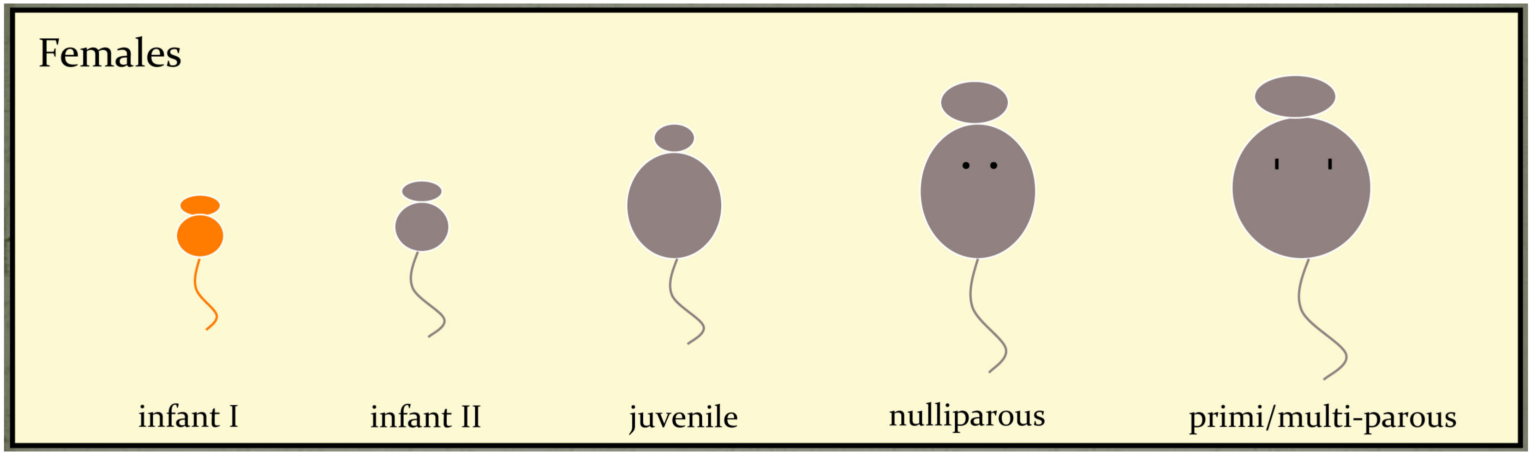
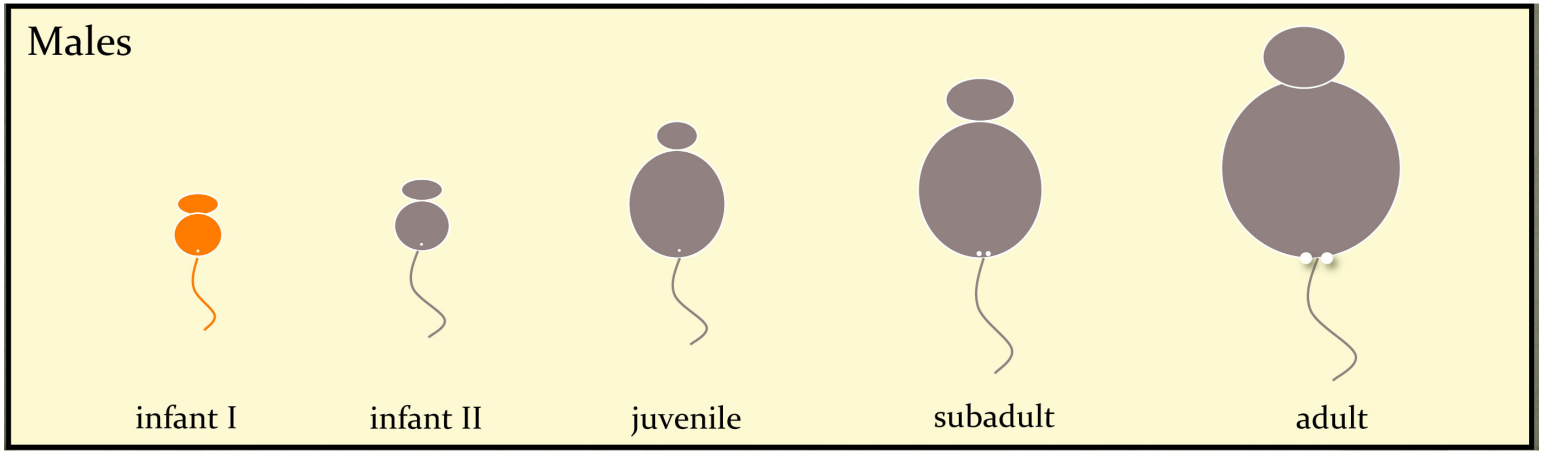
APPENDICES

Appendix 1 Sex and age class for female and male Phayre's leaf monkeys

Appendix 1a Female age and reproductive classification using color, size and nipple length



Appendix 1b Male age and reproductive classification using color, size, and testicular development



Appendix 2 Method of documentation of infant color change in skin and fur from infant I to infant II