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“PATERAL KINSHIP IN A MATRILICAL SOCIETY OF OLIVE BABOONS (*PAPIO
HAMADRYAS ANUBIS*) IN LAIKIPIA DISTRICT, KENYA”

By

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ABSTRACT OF THE DISSERTATION

Paternal Kinship in a Matrilocal Society of Olive Baboons (*Papio hamadryas anubis*) in Laikipia
District, Kenya

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Relationships with relatives are arguably the principal organizing feature of mammalian sociality. Studies of nonhuman primates, in particular, demonstrate the importance of kinship in the evolution of affiliative behaviors. The majority of these studies, however, have focused on relatedness expressed through the mother. Although all individuals have a father, less is known about the importance of paternal kinship. My dissertation seeks to expand our understanding of the role of *paternal* kinship in a matrilocal society by answering the following questions: 1) how do social bonds between different kin types vary?; 2) how does the presence of both mothers and fathers in groups influence the foraging behaviors of juveniles?; and 3) how do juveniles feed near same-aged peers of different kin types? I examined these questions using behavioral and genetic data collected on wild olive baboons (*Papio hamadryas anubis*) during a 14 month study in Kenya.

My research indicates that *both* maternal and paternal kinship play several important roles in the social and foraging behaviors of young baboons. First, paternal half-siblings maintained social bonds with one another of intermediate strength, i.e., weaker than those characterizing maternal half-siblings, but significantly stronger than the relations of unrelated conspecifics. Moreover, these bonds of paternal half-siblings were significantly stronger when their shared father was present in the group than when he was absent, suggesting familiarity through associating with the father is the mechanism underlying recognition of paternal half-siblings. This study also found that both mothers and fathers enhanced the foraging success of

juveniles under certain conditions. In resource patches likely to engender contest competition, juveniles fed for longer periods when mothers were present. For foods requiring skill to extract and consume, immatures fed longer when near a parent of the same sex. These data suggest that parents may: 1) mitigate the costs of feeding competition; and 2) facilitate the learning process for consuming difficult-to-acquire food. Finally, the foraging of immature baboons was also improved by the presence of paternal and maternal juvenile half-siblings. This study contributes to our understanding of the adaptive significance of kinship in expanding our understanding of the evolution of social behavior.

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INTRODUCTION

Over the past half a century, researchers have begun to understand the critical role that kinship plays in the lives of nonhuman primates. Primate societies are often composed of related individuals that maintain a cohesive social unit over time (Pusey and Packer 1987). This group composition increases the probability and frequency of interactions between kin, thus providing group members with the opportunity to preferentially interact with kin. This group structure facilitates the evolution of behaviors through kin selection (Silk 1987). Much work has already shown that kinship influences a wide variety of social behaviors among nonhuman primates (Gouzoules and Gouzoules 1987; van Hoof and van Schaik 1992; Silk 2002).

Until recently, however, most kinship studies were based on an observational understanding of relatedness. Maternal relatedness is much more easily determined through observed birth and nursing associations. Although many fundamental behavioral models rely on kinship to explain the evolution of social systems, observational research alone cannot elucidate all forms of kinship and, hence, the extent to which relatedness influences social behavior. Recent advances in the storage and extraction of noninvasively collected fecal DNA, as well as in genotyping techniques, now enable researchers to measure and evaluate *paternal* kinship.

The research presented here explores the social and foraging behaviors associated with paternal and maternal kin within a matrilocal society of olive baboons (*Papio hamadryas anubis*). Olive baboons provide an excellent model to evaluate relationships with both types of kin. While the social structure of this species is organized around matriline, like most Old World monkeys, where females remain in the natal group and males disperse, there remains an opportunity for paternal kin to interact. This is because male reproductive tenure can last from two to four years, and during this time a male may be able to monopolize copulations, creating a high reproductive skew. In this scenario, same-aged peers are more likely to be paternal half-siblings than individuals from different birth cohorts (Altmann 1979). Therefore, even in a matrilocal group

like that of the olive baboon, individuals, especially youngsters, may co-reside with both maternal *and* paternal kin.

This study focuses on the behavior of immature olive baboons. Compared to most other mammals, primates experience longer periods of immaturity before sexual maturation, yet this developmental stage is poorly understood (Walters 1987). Relationships formed during this period are critical to a youngsters survival (MacKinnon 2007) and are especially sensitive to group composition (Pereira and Fairbanks 1993). Understanding juvenile social and foraging behavior will expand our understanding of the ontogeny and evolution of social behaviors.

Here I explore the theoretical and empirical work that addresses the significance of kinship across and within primate societies. I first address the fundamental framework provided by kin selection theory and review how kinship affects affiliative behaviors. Next, I discuss variables that might limit the predictive power of kin selection theory and may therefore affect how we interpret empirical studies on primate behavior. Finally, I present future directions that kinship research may take and discuss novel questions that are just now beginning to receive attention in the literature.

Kin Selection Theory

Among the first and most fundamental insights regarding kinship was our understanding of altruism. This began when Darwin (1859) realized that altruistic behavior seemed to contradict his theory of natural selection because such acts tended to reduce an individual's fitness. Specifically, altruism is defined as an act that benefits the recipient at a cost to the actor. Three requirements must be met to ensure that an altruistic trait can evolve through kin selection. First, both actor and recipient of the altruistic act must share a portion of the genetic basis for altruism that is identical by descent. The probability of shared genetic material and benefit of the behavior (to the recipient) must offset the cost of the altruistic act. Second, these individuals must share the genotype that serves as the basis for the altruistic behavior. Third, these individuals must selectively interact with each other (Silk 1987).

W. D. Hamilton (1964) was the first to formulate an equation to determine when an altruistic act towards a relative will be beneficial. Hamilton's Kin Selection Theory provided new insights into the evolution of social behaviors. Coining the term "inclusive fitness," Hamilton proposed a measure of an individual's direct (through immediate reproductive success) and indirect (through the reproductive success of relatives) fitness. Kin Selection Theory predicts the circumstances under which kinship altruism will evolve and preferential treatment of kin is expected (Hamilton 1964). The equation, also known as Hamilton's rule, requires knowledge of three variables: the costs (**c**) to the actor's direct fitness; benefits (**b**) to the recipient's direct fitness; and the degree of relatedness (**r**) between the actor and the recipient. An individual is expected to behave altruistically when $c < b \cdot r$ (Hamilton 1964). This formula implies that altruism will occur when the fitness costs to the actor are less than the fitness benefits to the recipient, devalued by r , the coefficient of relatedness. Through kin selection, altruism is predicted to occur between related individuals and costly altruism should be limited to closely related kin (Silk 2002).

Kinship and Affiliation

Female Nepotism:

Female nepotism arises in a variety of nonhuman primate species, exhibiting varying degrees of reproductive skew, dispersal patterns, and social organization (Silk 2006). Female philopatric societies, in particular, have received a significant amount of attention regarding female nepotism because females will remain in their natal groups throughout their lives, spending a large amount of their time interacting with kin (Gouzoules and Gouzoules 1987). Since males routinely disperse, kin dyads are primarily composed of maternally or paternally related females. In addition, many kinship studies have focused on Old World monkeys, partly because females in these societies exhibit well-differentiated, stable relationships that are organized around matriline (Gouzoules and Gouzoules 1987; Walters and Seyfarth 1987). These maternal bonds endure for years (Bernstein 1991; Gouzoules and Gouzoules 1987; Walters and

Seyfarth 1987; Silk et al. 2006a,b), directly influencing affiliative behaviors, such as spatial association, grooming, and tolerated co-feeding (Gouzoules and Gouzoules 1987). These social relationships dramatically enhance reproductive success and overall lifetime fitness (Silk et al. 2003, 2006a, 2009, 2012).

With respect to coalitional behaviors, the decision of whom to support and who to target depends upon the costs of the interaction and the benefits incurred from the intervention. It is generally assumed that it is more beneficial to support kin and target nonkin because of benefits arising from kinship altruism and inclusive fitness (Silk 2002; Widdig et al. 2006a). Just like the distribution of affiliative behaviors, in many female philopatric societies, dominance and coalitional behaviors are influenced by matrilineal structure (e.g., Silk et al. 2004).

Dominance and coalitional behaviors in matrilineal societies begin to structure a female's behavior at infancy (Berman 2004). For instance, dominance acquisition in these societies takes the form of "youngest ascendancy," whereby daughters assume rank position below their mothers and in reverse order of their age (Hill and Okayasu 1996). Since the dominant sister is the youngest and, therefore, the smallest daughter, she will need "back up" from the older sisters she outranks, in particular, and other females, in general. This system requires a large amount of support from maternal kin (mother, aunts, etc.) to ensure the stability of the ranking system (Datta 1983; Chapais 1992; Chapais and Gauthier 1993). This biased support of kin continues through adulthood (Widdig et al., 2001, 2006a; Silk et al. 2006a,b).

In female philopatric societies, females are not only exposed to maternal kin, but also to paternal relatives. Although males routinely disperse, if male reproductive skew is high, age cohorts are likely to be paternal half-siblings (Altmann 1979). Patrilineal kinship, though, should be less extensive than matrilineal kinship since females do not reside with their father's kin (Chapais and Berman 2004). Although less work has been done to determine the significance of paternal kinship in matrilocal societies due to the technological difficulties of assessing paternity, there is some compelling evidence that suggests that females recognize and favor paternal kin

(see Widdig 2007).

Male Nepotism:

The kinship structures of patrilocal societies are essentially the converse of matrilocal societies and are therefore the most useful to consider when investigating male nepotism. Since males remain in their natal groups throughout their lives, they also have the opportunity to maintain relationships with both maternal and paternal kin. Because females disperse, however, the only maternal kin that should be available to a male are his mother and maternal brothers. Paternally related individuals should be more plentiful, because males remain and breed in their natal groups. Outside of mother-son dyads, males are not likely to be related to resident females. Therefore, in these social systems, nepotism is expected to be more prevalent among related males (Strier 1994).

Many New World primates exhibit male bonds (Strier 1990), although few studies have determined conclusively whether or not these relationships are based on kinship. It has been shown, however, that male relationships with kin in some species are positively correlated with reproductive success. For instance, both male muriquis (*Brachyteles arachnoids hypoxanthus*; Strier et al. 2002) and Peruvian squirrel monkeys (*Saimiri sciureus*) (Mitchell 1994) tolerate related males when mating. While male red howler monkeys (*Alouatta seniculus*) typically disperse, coalitions of paternally related males are more successful than nonrelated coalitions at taking over and defending social groups (Pope 1990).

Chimpanzees (*Pan troglodytes*) are often referenced as a prime example of kinship influencing male social behavior due to patrilocality (e.g., Goodall 1986; Watts 1998; Boesch and Boesch-Achermann 2000; Langergraber et al. 2014). Males cooperate with maternal brothers to compete for rank and access to females (Langergraber et al. 2007; Mitani 2009). In addition, males will cooperate with a variety of male relatives (e.g., fathers, sons, cousins) over territories (Langergraber et al. 2011; Mitani et al. 2010). Recent work has begun to challenge the assumption of patrilocality. For example, some have reported male-male relatedness was *not*

much higher than that of females (Gagneux et al. 2001; Vigilant et al. 2001; Lukas et al. 2005), and juvenile males have been observed to transfer with their mothers (Boesch et al. 2008). In general, though, these cases are considered rare in chimpanzee communities (Langergraber et al. 2014).

Although bonobos (*Pan paniscus*) exhibit weak male-male bonds (Nishida and Hiraiwa-Hasegawa 1987), genetic evidence reveals overall low within-group relatedness (Gerloff et al. 1999). The strongest bonds occur between related adult male-female half-siblings (Hohnmann et al. 1999) and mother-son pairs (Hohnmann et al. 1999; Surbeck et al. 2011). Such cross-sexual kinship bonds are able to evolve in bonobos because, unlike chimpanzees, this species exhibits a more egalitarian dominance structure (de Waal 1997; Hohnmann et al. 1999). Subsequently, adult females may have the social status required to offer adult males coalitionary support, while males may provide females with protection against infanticide or harassment (Hohnmann et al. 1999).

Beyond multimale-multifemale societies, male bonds and possible nepotism can also be found in species characterized by a harem system (one male and multiple females). The breeding male occasionally tolerates “follower” males, and this relationship may be affected by kinship. Specifically, fathers may tolerate the presence of sons since they help to defend the harem, and sons may bide their time until they may inherit the harem (van Hoof and van Schaik 1994). In mountain gorillas, sons were found to follow their father during group fissions, perhaps also utilizing the strategy of harem inheritance (Nsubuga et al. 2008).

In matrilocal species, even though male dispersal reduces the availability of male kin (Silk, 1992), dispersal is sometimes influenced by kinship (Cheney and Seyfarth 1983). Male rank relations in many Old World monkey species are often dynamic (de Waal 1985) where males may only occupy the highest rank for a short period only, making alternative tactics such as coalition formation critical to enhancing lifetime reproductive success (Bercovitch 1991; Danish and Palombit 2014). Old World male monkeys form temporary coalitions to take over consorts involving estrus females (Packer 1977) or will try to improve rank to increase access to females

(van Hoof and van Schaik 1992). In this scenario, biasing coalitionary behaviors towards any kin available would also provide immediate indirect fitness benefits (Widdig et al. 2000; Danish and Palombit 2014). Male Barbary macaques (Widdig et al. 2000) and bonnet macaques (*Macaca radiata*) (Silk 1992), for instance, preferentially support kin during conflicts.

Constraints on Nepotism

Despite the relative importance that kinship sustains across primate social systems, there are a range of proximate variables that may constrain the extent of kin biased behaviors. It is important to remember that kin selection predicts how unconstrained individuals *should* behave, not how they actually can or do behave (Chapais and Belisle 2004). To review, altruism is expected to be profitable when the ratio of c/b is greater than the degree of relatedness between two individuals. In other words, the values of c and b (which are contextually variable) determine the relatedness threshold for altruism (“threshold” from hereafter). However, determining how altruism should be distributed across kin that meet the threshold is problematic, as access to preferred types of kin can vary (Altmann 1979). So, while Hamilton’s (1964) equation is useful in determining the minimal degree of relatedness at which an altruistic act is profitable, it does not predict how individuals are practically able distribute their time and energy among kin (Chapais and Belisle 2004).

Three variables can potentially impose a strong influence on nepotistic encounters (Chapais 2001; Chapais et al. 2001; Chapais and Belisle 2004). First, time may alter the cost-benefit ratio, creating a situation where the equation for kin selection is no longer a static calculation. Altmann (1979), through an examination of grooming (as its benefits--such as ectoparasite removal--are likely to decrease over time), concluded that when the benefits for the recipient begin to decrease, it is advantageous for the actor to stop grooming that individual and begin to groom the next closest relative. The point of diminishing returns from a particular behavior will determine the optimal time spent engaging in that particular behavior with another individual, thereby dictating the number of kin within the threshold for the optimal amount of

time (Chapais and Belisle 2004).

Second, the availability of kin is a powerful determinant of the allocation of nepotism. Though it may be in the individual's best interest to favor a particular category of kin (for instance, the closest related kin in the group) for a certain altruistic act, the spatial availability of such kin will affect how altruism can be distributed. Additionally, the number of relatives occupying each kin category can also constrain an individual's ability to behave nepotistically. If an individual has a large number of close relatives in each kin category, it will maintain a large pool of potential close kin recipients and is therefore expected to have less time available to behave preferentially towards distant kin (Chapais and Belisle, 2004).

Finally, the type of relatedness that exists between the actor and potential recipient may also affect altruism. Chapais et al. (2001) found that while the threshold may rest at an r of 0.125 among direct kin (e.g., grandmother, mother), it may remain at 0.25 for collateral kin (e.g., siblings). The discrepancy of the threshold between direct and collateral kin may be due to proximate correlates (i.e. levels of familiarity) or fundamental aspects (i.e. dominance competition within matriline or patriline; Chapais et al., 2001). Either way, the r value alone does not account for how individuals respond to relatedness. This argument highlights how observed behaviors may deviate from theoretical predictions that assume optimal behaviors.

Future Directions

Beyond a more detailed understanding of maternal kinship, the next step in kinship research is to explore paternal kinship. As opposed to maternal relatedness, paternal kinship necessitates genetic analysis. Molecular methods and noninvasive sampling allow for field researchers to uncover complete relatedness patterns in wild populations. One question that is recently receiving attention, with the help of these new techniques, is: what are the proximate and ultimate functions, if any, of paternal kin in a matrilineal society?

There are two primary categories of paternal kin available to an individual in a matrilineal social group: 1) its father and 2) its half-siblings. The few studies of paternal kinship in

matrilineal societies provided intriguing indications that paternal kin provide agonistic support and protection (van Schaik and Paul 1996; Palombit et al. 1997; Alberts 1999; Borries et al. 1999; Buchan et al. 2003; Nguyen et al. 2009) and exchange affiliative behaviors (Widdig et al. 2001, 2002, 2006; Smith et al. 2003; Silk et al. 2006a, Charpentier et al. 2008, 2007). Among savannah baboons, for example, Smith et al. (2003) found that adult female baboons bias affiliative behaviors towards paternal half-siblings to the same significant extent as maternal half-siblings. Alternatively, Widdig et al. (2001, 2002) found that, among semi-free ranging rhesus macaques, while adult female paternal half-siblings are significantly more affiliative with each other than with unrelated dyads, maternal half-siblings exhibited stronger relationships. The authors proposed that kin selection must be “asymmetrically influential,” since maternal and paternal kin demonstrate different levels of social bonds (Widdig et al., 2002). It has been suggested that this difference in bond strength seen among paternal kin is the result of the different demographic conditions that occur in natural versus provisioned populations (Smith et al, 2003) or due to the availability of preferred social partners (Silk et al. 2006).

While the mechanisms involved in paternal kin identification are beyond the scope of this paper, investigating the types of individuals that modify their behavior according to paternal kinship can shed light on the evolutionary significance of such behavior. For example, age similarity has been offered as a possible proxy used to identify paternal kin (Altman 1979; Alberts, 1999; Widdig et al., 2001; Smith et al., 2003). This assertion rests on the fact that in multimale-multifemale societies, mating can be monopolized by one or a small number of males. Individuals conceived during the same reproductive season are likely to be paternal half-siblings due to the correlation between male rank and reproductive success (Altmann, 1979; Altmann et al., 1996; de Ruiter and Geffen, 1998; Widdig et al., 2004). This mechanism, however, is not consistently demonstrated across studies examining paternal kinship (reviewed by Widdig 2007).

There is evidence suggesting that a broader range of individuals, besides those of the same age cohort, are able to recognize paternal kin. Excluding the confounding effects of spatial

proximity, studies suggest males are able to identify and care for their offspring (Buchan et al., 2003). Moreover, in accordance with Widdig et al. (2001, 2002), Charpentier et al. (2007) found asymmetry across relatedness categories in a group of semi-free ranging mandrills. Juvenile mandrills were shown to prefer older maternal and paternal relatives as compared with nonkin. However, among dyads of juveniles, maternal half-siblings demonstrated significant levels of affiliation while paternal half sibs and nonkin did not. The authors speculate that this may be the result of kin discrimination operating in adults as opposed to youngsters. Perhaps the adult males are able to distinguish genetic offspring by tracking copulations. Indeed, the exact mechanisms driving paternal kin recognition are not yet clear and will not be examined in this study.

Studies of paternal kinship in matrilineal societies have also touched upon the adaptive significance of such forms of relatedness. Charpentier et al. (2008) reported that, in yellow baboons, the father's presence in the social group is associated with both male and female offspring reaching maturity at a younger age, potentially increasing the offspring's lifetime reproductive success. However, the effect was only seen in young males if the father was high ranking at the time of the birth. Charpentier et al. could not explain precisely how a father's presence might accelerate maturation, but they suggested two possible mechanisms. First, fathers can offer protection during agonistic disputes (Buchan et al. 2003; Lemasson et al. 2008; Moscovice et al. 2009; Nguyen et al. 2009) and against infanticidal or predatory attacks (Busse and Hamilton, 1981; Palombit et al. 1997; Borries et al. 1999). This male defense may reduce stress of youngsters, providing a "buffered" social environment, thereby inducing faster development. Second, fathers may enhance the quality and quantity of food acquired by their offspring, which may improve growth and maturity rates (Bercovitch and Strum 1993; Altmann and Alberts 2005). Huchard et al. (2013) tested the latter hypothesis and found that father-offspring associations are more frequent when the juveniles are feeding, and such activities enable the youngsters' access to larger food patches. More work, however, must be done to better understand the ultimate significance of relationships with paternal relatives.

The research presented here attempts to build on these works by exploring social and foraging behaviors associated with both maternal *and* paternal kinship in a matrilocal species. First, I examine the social bonds among young olive baboons (*Papio hamadryas anubis*) and consider the influence of mothers and fathers on these relationships. I then evaluate the foraging behaviors of these immatures and suggest the importance of different types for resource acquisition. Finally, I draw conclusions on this research and suggest avenues for future studies.

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Chapter One

Availability of parents determines social bonds between maternal and paternal half-sibling immature olive baboons (*Papio hamadryas anubis*)

1. INTRODUCTION

Over the past half a century, the importance of kinship in the evolution of social behavior has become increasingly clear. Primate societies are typically composed of related individuals that maintain cohesive social units over time (Pusey and Packer 1987; Hill 2004). This distinctive group composition creates pathways for behavior to evolve through kin selection (Silk 1987). Much work has shown that kinship influences a variety of social behaviors (Gouzoules and Gouzoules 1987; van Hoof and van Schaik 1992; Silk 2002; Chapais and Berman 2004; Langergraber 2012).

Kin selection theory (Hamilton 1964) predicts that relatives will generally be disproportionately represented as targets of individual altruistic and affiliate behavior, but the distribution of kin-directed behavior depends in part upon the availability of kin as interactants (Hill 2004), in terms of both the abundance and spatial distribution of relatives of various kin categories (Chapais et al. 1997, 2001; Chapais and Belisle 2004). For example, all else being equal, a sibling that shares both parents with the actor (i.e. a full sibling) is a more preferable partner than one that shares only one parent (i.e. a half-sibling) because the probability of sharing the same genes is greater in the former case (coefficient of relatedness $r=0.5$, compared to $r=0.25$ for the latter). If full siblings are not present in a group, however, an individual might be expected to direct altruistic behaviors towards the less preferable kin type (assuming equivalent efficacy of kin recognition). In theory, if an individual has access to a large number of close relatives present in a group, it will invest more of its time and energy interacting with those individuals than more distantly related kin. Indeed, constraints on time and energy (as well as the relative costs and

benefits of each scenario) are likely to restrict the ability of an individual to equally distribute affiliative behaviors across relatives. Instead, an individual is predicted to preferentially direct nepotistic behavior towards those that share a relatively higher probability of having identical genes by descent (Hamilton 1964; Chapais and Belisle 2004).

Given these constraints, and as predicted by kin selection theory, adult female cercopithecines tend to restrict strong social ties to a small subset of available females (Silk et al. 1999, 2006a, 2010a, 2012), typically close maternal kin (e.g. mothers and daughters [Silk et al. 2006b]). These relatives maintain close spatial associations and exchange affiliative behavior (e.g., grooming [Sambrook et al. 1995; Henzi et al. 1997; Silk et al. 2006a,b]) to a greater degree than is observed with nonkin or with more distant maternal kin (such as nieces and aunts). Some studies provide evidence that social integration, achieved through these relationships, are also positively correlated with lifetime reproductive success (Silk et al. 2003, 2009) and longevity (Silk et al. 2010b).

While many studies of primates have focused on the interactions among maternal kin, few have resolved the potential influence of paternal kinship on social strategies. There are two good reasons for this emphasis. First, many monkey groups—particularly in the Old World—are organized around matriline, female philopatry, and male dispersal (Pusey 1987; Strier 1994; Di Fiore and Rendall 1994; Hill 2004; Cords 2012). Second, maternal relatedness is easily assigned by researchers through observations of births. Although all individuals have a father, less is known about the importance of paternal kinship in affiliative interaction. Notably, Hamilton's equation highlights the probability of sharing a gene as an important determinant, not whether it is inherited from the mother *or* father. Thus, *ceteris paribus*, paternal kin are theoretically expected to distribute altruistic behavior in the same manner as maternal kin.

To date, a few studies have explored affiliative behavior among paternal relatives in matrilineal primate societies (rhesus macaques, *M. mulatta*: Widdig et al. 2001, 2002, 2006; Schülke et al. 2013; yellow baboons, *P. h. cynocephalus*: Alberts et al. 1999; Buchan et al. 2003;

Smith et al. 2003; Silk et al. 2006b, Charpentier et al. 2008; mandrills, *Mandrillus sphinx*: Charpentier et al. 2007, 2008, 2012). While these studies suggest that individuals preferentially associate with paternal kin, the patterns observed vary. Some researchers report that paternal half-sisters maintain social bonds that are equivalent in strength to those of maternal half-sisters (Smith et al. 2003), while others describe paternal bonds of intermediate strength between those of maternal kin and nonkin (Widdig et al. 2001, 2002; Silk et al. 2006a).

In an attempt to resolve these varying results, some researchers have suggested that adult females potentially target close maternal kin, such as mothers and daughters, for social interactions, but when such kin are not available, they may form compensatory strong bonds with paternal kin (Smith et al. 2003, Silk et al. 2006b), strengthen existing bonds with maternal half-sisters (Silk et al. 2006b, Engh et al. 2006), or form strong bonds with nonrelatives who occupy similar ranks (Silk et al. 2006b). These hypotheses generate predictions about how adult females will interact with relatives when preferred partners are no longer available. For example, in a small group of yellow baboons, females who lacked mothers were more likely to have stronger relationships with paternal and maternal half-sisters (Silk et al. 2006b). Similar results were reported by others (Smith et al. 2003; Engh et al. 2006). Together, these results suggest that demographic conditions affect the strength of social bonds among paternal siblings.

Male cercopithecines interact affinitively with infants through various behaviors, such as grooming, carrying, agonistic support during conflicts, or protection from infanticide (van Schaik and Paul 1996; Palombit et al. 1997; Alberts 1999; Borries et al. 1999; Buchan et al. 2003; Nguyen et al. 2009), and recent work has begun to suggest that the presence of a father within the group can positively influence an offspring's reproductive success (Charpentier et al. 2008; Huchard et al. 2012). However, how fathers influence the social behaviors of developing immatures remains poorly understood (Widdig 2007).

Building upon these studies (e.g., Silk et al. 2006b; Charpentier et al. 2008), the research reported here examines the role of father presence on the social bonds between paternal half-

siblings. Maternal relatives may be preferred social partners generally, but the presence of fathers may also impact the types of bonds an individual maintains within a group. Specifically, the presence of a shared father may facilitate familiarity among his offspring (*sensu* Widdig 2007), subsequently promoting the development of stronger social bonds among paternal half-siblings.

This study focuses on the individuals who arguably have the most to gain from the presence of mothers and/or fathers in their social group: juveniles. This age class serves as an excellent model for evaluating the possible effects of available kin on social bonding in primates. Compared to most other mammals, primates experience longer periods of juvenility and adolescence, during which they acquire many skills necessary for survival and reproduction, including foraging, predator avoidance, and, most notably in the current study, social strategies (Pereira and Fairbanks 1993; Lonsdorf and Ross 2012). Depending on their sex, individuals reaching social maturity either leave their natal group or integrate themselves into the local social world. With the notable exceptions of hamadryas (*P. h. hamadryas*) and apparently Guinea (*P. h. papio*) baboons (Fickenscher et al. 2011; Kopp et al. 2014), most baboons (*P. hamadryas* subsp.) are characterized by male dispersal and female philopatry. Thus, it is during the juvenile period that possible effects of fathers on offspring social relationships may be particularly detectable and, perhaps, crucial.

This study tested the following predictions:

P1) Social bond strength will differ between different types of immature dyads: maternal half-siblings, paternal half-siblings, and unrelated pairs.

P2) Immatures whose mother are present in the group will: (P2a) maintain stronger social bonds with maternal half-siblings than with paternal half-siblings, (P2b) maintain a greater number of strong social bonds with maternal half-siblings than with paternal half-siblings.

P3) Immatures whose mother is not present in the group will: (P3a) maintain stronger social bonds with paternal half-siblings compared to those with mothers; (P3b) maintain an equal

number of strong social bonds with both paternal and maternal half-siblings.

P4) Compared to immatures without fathers present in the group, immatures with fathers present will maintain: (P4a) stronger ties with paternal half-siblings; (P4b) a greater number of strong social bonds with paternal half-siblings; (P4c) fewer strong bonds with maternal half-siblings; and (P4d) weaker bonds with maternal half-siblings .

These predictions derive from the aforementioned studies of baboons (i.e., Smith et al. 2003; Silk et al. 2006b; Engh et al. 2006), which suggest that the absence of a preferred maternal relative will promote greater investment in maintaining compensatory bonds. Because the subjects of this study are not yet of reproductive age and therefore do not have offspring of their own, the preferred maternal relative is likely to be the mother. As proposed by Silk et al. (2006b), these compensatory bonds should include both maternal *and* paternal half-siblings. In contrast, when a mother is present, individuals should not expand their social network to incorporate paternal kin and should instead maintain close ties with maternal relatives only. This is because the predicted preference for maternal relatives (Silk et al. 2006b) will tend to limit social interactions to the small subset of individuals meeting this criterion (Henzi et al. 1997, Silk et al. 1999, 2006a, 2010a, 2012).

A natural but unexpected demographic change in the study group provided a better opportunity to assess differences in social bonds between immatures with and without mothers. An apparent predation event resulted in approximately half of the focal subjects losing their mothers within a roughly three month period. This relatively rare occurrence provided an unusual opportunity to examine behavioral differences between immatures with and without mothers in the field.

The explicit focus of this research on the behavior and bonds of *immature* primates is likely to provide valuable insights beyond those obtained solely through study of adult females. First, immature individuals are likely to have greater potential access to half-siblings than do adults (due to the presence of pre-dispersal young males). Moreover, study of juveniles allows better

analysis of interactions among paternal kin in relationship to the presence of a shared father.

2. METHODS

Field site and Subjects:

I studied 45 immature individuals in one habituated group of olive baboons (n=111) in the Laikipia District, Kenya that has been studied by Dr. Ryne Palombit since 2001. Generally, “juveniles” and “subadults” are categorized within a life stage that commences with weaning and terminates with sexual maturity (Pereira and Altmann 1985; Pereira and Fairbanks 1993). Thus, no immatures in this research were observed nursing from their mothers, engaging in sexual consortships, or displaying secondary sexual characteristics, such as testicular descent for males or sexual swellings for females. In those cases where an individual developed one or any of these diagnostically adult characteristics, data collection on it ceased.

Within the original focal group, there were 23 females and 22 males. Six of these individuals were ultimately excluded from analysis, either because of inconclusive genotyping (N=3) or because they disappeared or matured before sufficient behavioral observations could be made (N=3). The final set of subjects thus included 19 females and 20 males.

Behavioral Data:

I collected behavioral data and fecal samples from April 2010 through June 2011. Daily observational data were typically collected between 0700 and approximately 1400. Each focal individual was selected at random (via a list generated by a computer program), and 10-minute focal animal samples (Altmann 1974) were collected. During focal sampling, I continuously scored three categories of social behaviors (affiliative, agonistic, polyadic) and activities (e.g., rest, feed [by item], travel). Spatial data were collected in two ways. I continuously recorded all movements that brought the focal individual and any other individual to within 2m of one another; the identity of the individual responsible for this “approach” was noted. I also continuously recorded when this “close proximity” was terminated as either the focal subject or the other individual moved beyond this 2m range; the identity of the individual responsible for

this “withdrawal” was noted. In addition, at two minute intervals, the identities of all baboons within 6m of the focal individual were recorded instantaneously. In total, I collected approximately 6,800 focal samples over the course of 1,115 hours of observation from 39 immatures.

Predation Event Affecting Group Composition:

The field component of this project provided a rare and unanticipated opportunity to analyze the effects of parental presence and absence on juveniles’ social bonds with one another. During a relatively short period (approximately two months), twelve adult females, five subadult females, and five adult males all disappeared from the study group. Several lines of concurrent evidence implicated leopard predation as the likely cause: new claw marks were seen on the baboon troop’s sleep trees, the physical remains of baboons were found near these trees, and local residents reported hearing nocturnal leopard vocalizations (Danish et al., *in prep*). The change in group composition that resulted from these disappearances presented a “natural experiment” on the effect of loss of a parent on immature social relationships. Although the timing of this predation event vis-à-vis my research schedule prevented a “before-after” temporal comparison of the same individuals’ behavior (due to the timing of my arrival at the field site), it did generate a large sample of immatures who no longer had their mother residing in the group. The social bonds of these individuals could be compared with other subjects whose mothers remained in the group. Moreover, since five potential fathers disappeared as well, a similar analysis of immatures with and without fathers in the group was possible.

Genetic Analysis:

I collected a total of 111 fecal samples from juvenile and subadult animals for PCR-based microsatellite marker genotyping. I also collected several high quality genetic samples (i.e., blood samples from deceased baboons in the study area, N=2) to use as a positive PCR control. By the end of the study, approximately three DNA fecal samples had been collected for every individual (mean=2.8; S.D=0.7; range=1-4). Fecal samples were collected in the buffer *RNAlater*®

(Ambion, Inc.), which stabilizes and protects cellular DNA *in situ*. At collection time, feces and RNAlater were combined at a roughly 1:10 ratio. After collection, samples were stored in the field at -4°C in a propane freezer. Samples were then shipped back to the U.S. at room temperature and refrozen upon arrival.

Extraction of DNA from the fecal samples and PCR-based place genotyping were performed in the Molecular Primatology Laboratory at New York University and in the Primate Molecular Ecology and Evolution Laboratory at the University of Texas at Austin. Using a QIAamp DNA Stool Mini Kit (Qiagen), I extracted and purified DNA from the fecal samples.

I used a modified version of the manufacturer's "Isolation of DNA from Stool for Human DNA Analysis" protocol available from Qiagen. Briefly, a sample of 200µl was first vortexed then lysed in Buffer ASL for 24 hours at room temperature on a rocking platform. This protocol also added 20 minutes to the incubation time recommended by Qiagen (Moscovice et al. 2009). Finally, unlike the published protocol, the DNA was left to incubate at room temperature for 30 minutes before elution in 100µl of Buffer AE.

This protocol was used consistently unless an extraction was determined to not amplify well in initial PCR trials. In these cases, the same procedure was followed using multiple 200µl aliquots from the same fecal sample that were combined during the binding stage of the protocol. This approach is useful for eliminating contamination and detecting allelic dropout and false alleles. This technique, in other words, consists of multiple extractions from the same sample as well as multiple samples from the same animal.

Primers for this study were tested and screened by a colleague (see Danish et al. *in prep*) and myself, based upon previous work done on other cercopithecine species (rhesus macaques [*Macaca mulatta*]: Widdig et al. 2001, 2002; yellow baboons [*Papio h. cynocephalus*]: Buchan et al. 2003; Alberts et al., 2006; chacma baboons [*Papio h. ursinus*]: Moscovice et al. 2009) and consultation with Dr. Di Fiore. As false alleles are more common in dinucleotide repeat microsatellite loci (Taberlet et al. 1995; Morin et al. 2001), tetranucleotide repeat sequences were

preferred. Primers were tested on individuals that were not related and only those producing detectable variation among the loci were used. Of the following 10 primers used, 8 display a tetranucleotide repeat sequence and 2 display a dinucleotide repeat sequence: D1s548, D2s119, D2s1236, D3s1766, D4s243, D5s111, D5s1457, D6s111, D11s2002, and D14s304.

Paternal kinship was assessed by genotyping all resident group members (n=111) using the aforementioned 10 microsatellites. Because fecal samples had been collected from many group individuals over many years preceding this, I was able to genotype adults that were not present during the time of *this* study but had been in the group at some point between 2011 and 2003 (N=31); these individuals represent possible parents of the study subjects.

Multiplex PCR is recommended to obtain more results from limited DNA, as multiple loci can be amplified from a single reaction (Taberlet et al. 1996). Once all allelic patterns were identified for all primers (performing PCR on each one individually), primers that amplified two to three different loci were then combined into a single PCR reaction (which required that those used shared similar annealing temperatures). If the product amplified in any unusual or difficult to read manner, the combination was no longer used. All reactions used primers with different fluorescent labels.

The PCR mix for the ten microsatellites was as follows: 1) 2.5 μ l of 2X Multiplex Mix (from Qiagen Multiplex PCR kit); 2) 0.5 μ l of Bovine Serum Albumin (BSA; 5.5mg/mL); 3) 1.0 μ L of a mix of primers for each of 1 to 4 loci (this mix includes adding RNAase free water to a stock solution of 10 μ M achieve a final concentration of 0.1-0.2 μ M); 4) 1.0-2.0 μ l of unquantified DNA template. BSA was used since it binds compounds that often reduce amplification of target DNA (Morin et al. 2001) and, for some cases where amplification was troublesome, the amount of BSA was increased by 0.5 μ l. The volume of the DNA template was also increased at times, in response to low amplification. Therefore, the final volume of the PCR reaction ranged from 5.0-6.0 μ l. The cycling conditions were as follows: 1) initial denaturation at 95°C (hot start) for 15 minutes; 2) then 36-40 cycles of 94°C for 30 seconds; 3) annealing temperature for 1.5 minutes (temperatures

varied for each primer, see Table 1.1); 4) 72°C for one minute; and 5) final extension at 72°C for 30 minutes.

Table 1.1 Annealing temperatures used for each primer.

Primer	Annealing Temperature
D1s548	55°C
D2s1326	55°C
D2s119	53°C
D14s306	53°C
D3s1766	57°C
D4s243	57°C
D5s111	55°C
D11s2002	55°C
D5s1457	55°C
D10s611	55°C

The PCR products were then separated and visualized on an ABI 3730 DNA Analyzer (Applied Biosystems). To do this, 1 µl of the PCR product was added to 9 µl of size standard-Rox mix (0.15 µl of GeneScan 500 ROX™ size standard and 8.85 µl of HiDi formamide). The reaction was then electrophoresed through a capillary filled with POP-7™ polymer to separate fragments of different sizes. The raw output data were analyzed by using GeneMapper v4.0 (Applied Biosystems). Alleles were assigned to individuals only if the output was within one base pair in length of the allele in question and if the peak height was higher than the size standard. If these criteria were not met, the results were excluded and a new PCR was conducted.

When working with DNA extracts of low concentration, such as those used in this study, stochastic sampling errors may occur (Taberlet et al. 1996). In this scenario, it is possible that a heterozygote amplifies at only one allele. Accordingly, an individual may then be incorrectly identified as a homozygote. This failure is referred to as “allelic dropout”. Allelic dropout has been found to occur more often in extract samples of low concentration (Morin et al. 2001). To mitigate this issue, all heterozygous genotypes were confirmed after a minimum of two replicates and all homozygous genotypes were confirmed after a minimum of four replicates (Moscovice et al. 2009).

Parentage assessments were conducted using a maximum likelihood approach, implemented using the software Cervus 3.0. Individuals with the highest log-likelihood ratio (LOD score) were assigned. This ratio represents the likelihood of parentage for a particular individual divided by the likelihood of parentage for a random individual. When multiple loci are incorporated into the analysis, the likelihood ratios are derived for each locus, multiplied together, then the natural log is taken. If two individuals are assigned the same LOD score, neither is assigned parentage.

No locus deviated significantly from Hardy-Weinberg equilibrium expectations, which suggests that nonamplifying or null alleles are not found at these loci. At lower frequencies, null alleles are more difficult to detect but may be accounted for in the error rate. Therefore, in all CERVUS simulations, I assumed the proportion of mistyped loci was 0.02. This rate is based on known mother-infant mismatches where 9 mother-infant pairs were compared across 10 loci (L. Danish *pers. comm.*). Parentage simulations were run assuming a pool of 37 candidate mothers and 41 candidate fathers for each immature and I assumed these candidates represented 95% of the total possible candidate parent pools. To assign parentage, I first assigned mothers and then used these results as the known dam to assign paternity. Confidence levels for the parentage assignments were obtained through simulating parentage for 100,000 offspring based on allele frequencies derived from the focal population. The confidence level is the average probability

that the assignment is correct using the critical LOD scores estimated by the simulation. For example if the average confidence level is 95%, you would expect of every 20 assignments at that confidence level, 19 would be correct and one would be wrong. Generally, using the CERVUS output, I did not accept assignments with less than 95% average confidence.

Some exceptions were made, however, based on demographic data. Following Van Horn et al. (2008), I focused my analysis on dyads where kinship could be inferred from either pedigree (e.g., matriline status is well known due to long-term observational data [Palombit, unpublished]) or demographic data (e.g., an immature and an adult male are not related if the adult male was not in the group during time at which the immature is likely to have been conceived). In the end, four immatures were excluded from the analysis because either the candidate fathers or mothers were excluded by at least one locus (and could therefore not be confidently assigned) or neither were present in the group or appeared old enough to be the parent. The final maternity and paternity assignments for the subjects are listed in Table 1.2.

Table 1.2. Maternity and paternity assignments for all focal individuals.

Juvenile Name	Juvenile Name Code	Mother Name	Mother Name Code	Father Name	Father Name Code
Erick	EK	Kate	KT	Arnie	AR
Vorick	VK	Velma	VL	Arnie	AR
Europa	EP	Kate	KT	Bob	BO
Yassin	YN	Yolanda	YO	Christopher	CT
Bosco	BC	Bernice	BE	Ernest	EN
Brandy	BD	Yolanda	YO	Ernest	EN
Cappuccino	CP	Victorya	VY	Ernest	EN

Table 1.2. Continued.

Juvenile Name	Juvenile Name Code	Mother Name	Mother Name Code	Father Name	Father Name Code
Dakar	DK	Doris	DO	Ernest	EN
Aurora	AU	Bernice	BE	Fred	FD
Felix	FE	Mikayla	MA	Fred	FD
Sophie	SO	Agnes	AS	Henry	HY
Suliwan	SW	Sandy	SA	Henry	HY
Wilbur	WB	Whoopie	WH	Henry	HY
Beverly	BV	Bernice	BE	Jake	JE
Panga	PG	Stella	SL	Judd	JD
Poseidon	PO	Mikayla	MA	Judd	JD
Waka	WK	Florence	FL	Judd	JD
Ewoton	EO	Mikayla	MA	Kevin	KV
Jack	JA	Judy	JU	Kevin	KV
Alicya	AY	Florence	FL	Mark	MK
Aladdin	AD	Loraine	LO	Murry	MR
Denzel	DZ	Doris	DO	Murry	MR
Eiffel	EI	Kate	KT	Murry	MR
Gertrude	GT	Victorya	VY	Murry	MR
Suzie	SZ	Sandy	SA	Murry	MR
Peter Jenkins	PJ	Phoebe	PH	Nelson	NL
Xerox	XE	Bernice	BE	Nelson	NL
Avon	AO	Velma	VL	Roy	RO
Cookie	CK	Cassie	CA	Roy	RO
Nicolas	NC	Norma	NO	Roy	RO
Nathalie	NT	Norma	NO	Roy	RO
Shurby	SU	Stella	SL	Roy	RO
Xanadu	XA	Norma	NO	Roy	RO
Yavie	YV	Yolanda	YO	Seymour	SE
Claire	CC	Cassie	CA	Sylvester	SV
Yazmin	YZ	Yolanda	YO	Sylvester	SV
Irene	IE	Zelda	ZA	Ted	TD
Kiwi	KW	Thelma	TL	Ted	TD
Fabian	FB	Stella	SL	Vortigern	VO

Types of Dyads and Individuals Used in the Analysis:

Based on my parentage results, I assigned dyads of immatures to one of four categories of kin group type: maternal half-siblings, N=30; paternal half-siblings, N=43; unrelated dyads, N=668; and full siblings, N=4. Because the sample size for full siblings was much smaller than the other categories of kin, this kinship category was not analyzed here. When two individuals did not share mother, father, or both, were categorized as “unrelated”.

Not all parents were present in the group during the time of this study. Ten females who had given birth to 18 of the focal individuals were not in the group during part or all of the study period. Six of these females (the mothers of nine immatures) were already missing from the study group when data collection commenced. Another four females (the mothers of nine immatures) disappeared during the predation event shortly after the study began. These mothers were therefore categorized as “absent” in the analysis.

In addition, the fathers of 31 focal individuals were not present in the group during part or all of the study period. Eleven males (the fathers of twenty-two immatures) were already missing from the study group when data collection commenced. Another three males (the fathers of nine immatures) disappeared during the predation event. These adult males were categorized as “absent”.

The other adult males and females who were in the group with their immature offspring were therefore categorized as “present” in the analysis.

Composite Sociality Index:

Following Silk et al. (2012), I used the *Composite Sociality Index* (CSI) to quantify the strength of affiliative relationships among the focal individuals. The CSI values were determined using the following formula: $([G_{ij}/G_{xy}] + [P_{ij}/P_{xy}])/2$. The term G_{ij}/G_{xy} represents the adjusted rate of grooming for the dyad ij divided by the mean frequency of grooming for all dyads within the group during the study. The second term, P_{ij}/P_{xy} similarly adjusts the frequency of proximity

maintenance (time spent within 6m) for dyad ij divided by the mean frequency of proximity for all dyads in the group during the study. CSI scores, therefore, represent the extent to which each dyad deviates from the mean for all other dyads within the group. While the mean is 1, the values of the score can range from 0 to infinity.

For the hypotheses addressing the strength of a social bond, the value of the CSI score for a dyad allows comparisons across kin groups (e.g., comparing the CSI values for paternal half-siblings vs. maternal half-siblings). The higher the CSI value for a dyad, the stronger the social bond between the two individuals constituting the dyad. As the distribution of CSI strengths were similar to those reported by Silk et al. (2006), I used the same arbitrary cut-off to operationally define “strong bonds”: dyads that exhibited a CSI within the top 10% (or exhibited a CSI value of 2.0 or higher). The number of strong bonds each immature subject maintained with individuals in each kin type was evaluated as well.

Although it is possible to revise CSI in numerous ways to accommodate age of focals, I use this measurement for three reasons. First, to compare directly with the studies of Silk and colleagues, it is important to use the identical methodology. Second, rates of affiliative interactions, as evaluated by this equation, are often used as proxies for relationship quality among nonhuman primates (Aureli et al. 2012). Third, the behaviors examined by the CSI (proximity and grooming) are still relevant to the age class examined here.

Statistical Analysis:

A permutation test (Pitman 1937) was used to examine if the observed value of the difference in the median CSI scores between groups is unreasonable given the distribution of this difference under the null hypothesis. To obtain the exact distribution, every possible permutation must be used, which is not feasible in this case due to the large sample size. Instead, CSI scores were assigned to a random permutation of the grouping variable of interest (the dependent variable), and the difference between the medians in these permuted groups was computed. This process was repeated 100,000 times in each case, which provided an approximation of the distribution of

the null hypothesis, which states that these groups come from the same distribution. If the observed value of the nonpermuted difference between group CSI medians exceeded 95% of the permuted ones, the groups were considered different. Because of this, for each test, the comparisons are reported here as p-values, which represent the proportion of permuted differences greater than the observed difference, so a “p-value” under 0.05 means that it exceeds 95% of the permuted distribution.

For these tests, the CSI score (a continuous variable) was the dependent variable. The following served as predictor variables for the tests: kin type (i.e. paternal half-siblings, maternal half-siblings, and unrelated) and the presence of a parent in the group (this was characterized as a binary variable, 0 or 1).

For the figures reporting medians presented below, bootstrapped confidence intervals were obtained by sampling the dataset with replacement many times, computing the median of each sample, and using the resulting sampling distribution of medians to compute the appropriate quantiles.

To examine the number of strong bonds an immature individual maintained across kin types, I followed Silk et al. (2006b) in examining the dyads characterized as “strong bonds”. Using this criterion, the immatures maintained a mean of 4.4 (S.D.=2.7, range=0-12) strong bonds with other immatures over the course of the study. To test the correlation between the presence of a father and the types of kin with whom an individual maintained strong bonds, I used a generalized linear model (GLM) with a Poisson log linear distribution because the number of bonds can only be counted as whole integers. Here, the dependent variable was the number of strong bonds an individual maintained and the predictor variable was a father’s residency in the group (this was a binomial variable characterized by 0 or 1).

To control for variation in the availability of relatives of different kin types to subjects, I divided the number of bonds an immature had with each kin type by the total number of

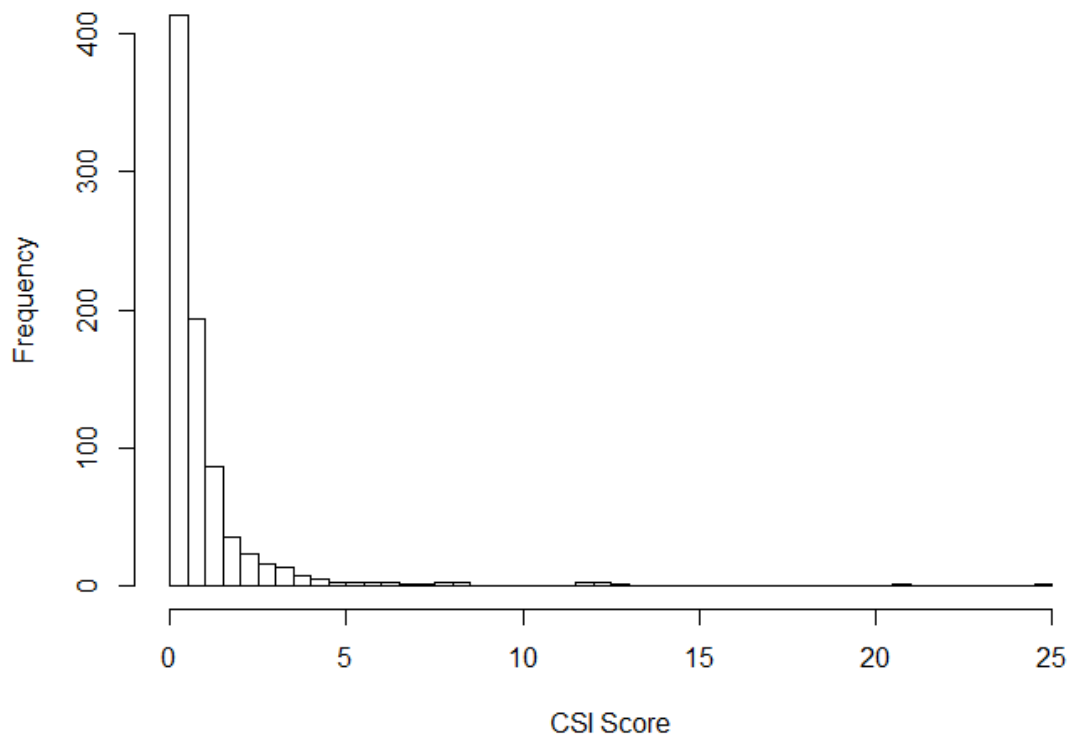
individuals of that kin type available (e.g., number of strong bonds with maternal half-siblings/number of maternal half-siblings available). The term “available” is defined as the number of individuals present in the group. This measure is able to demonstrate how individuals form strong bonds with different kin types. All statistical tests were two-tailed. R 3.1.3 was used to graph and analyze the data.

3. RESULTS

a. Magnitude of variation in social bond strength

I computed the CSI for all dyads within the sample (N=820, see Figure 1.1). To describe the data, the mean score for CSI values was 0.98, the median was 0.43, the mode was 0.11, and the standard deviation was 1.8. While the maximum score was 24.52 and the minimum was 0, only 10% of dyads exceeded a score of 2.0. This result demonstrates that most immature dyads were characterized by comparatively weaker rather than stronger bonds.

Figure 1.1. *The frequency distribution of observed Composite Sociality Index (CSI) scores among immatures.*



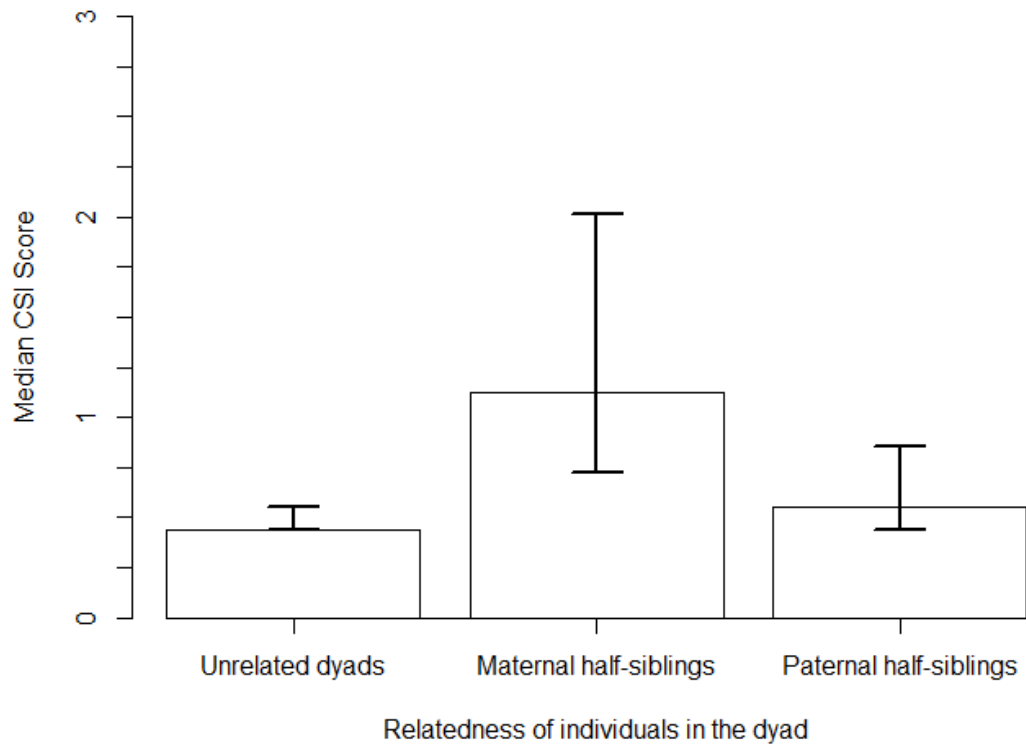
b. Social bond strength varies across kin categories

Prediction P1—that social bond strength differs between dyad categories—was supported. I found that the median CSI scores differed significantly across all three kinship categories of dyads (maternal: $N=30$ vs. unrelated: $N=668$; $p<0.001$; paternal: $N=43$ vs. unrelated, $p<0.05$; maternal vs. paternal, $p<0.01$; Figure 1.2, Table 1.3).

Table 1.3. Genealogical data and Composite Sociality Index (CSI) scores

Relatedness within dyad	Mean CSI	Median CSI	Std. Deviation	N
Unrelated dyads	0.81	0.44	1.11	668
Maternal half-siblings	3.57	1.12	6.05	30
Paternal half-siblings	1.76	0.55	3.08	43

Figure 1.2. *Strength of social bonds in different kinship dyads. Unrelated dyads, N=739; Maternal half-sibling dyads, N=30; Paternal half-sibling dyads, N=50. Error bars were computed by finding 95% confidence intervals for the bootstrapped medians.*

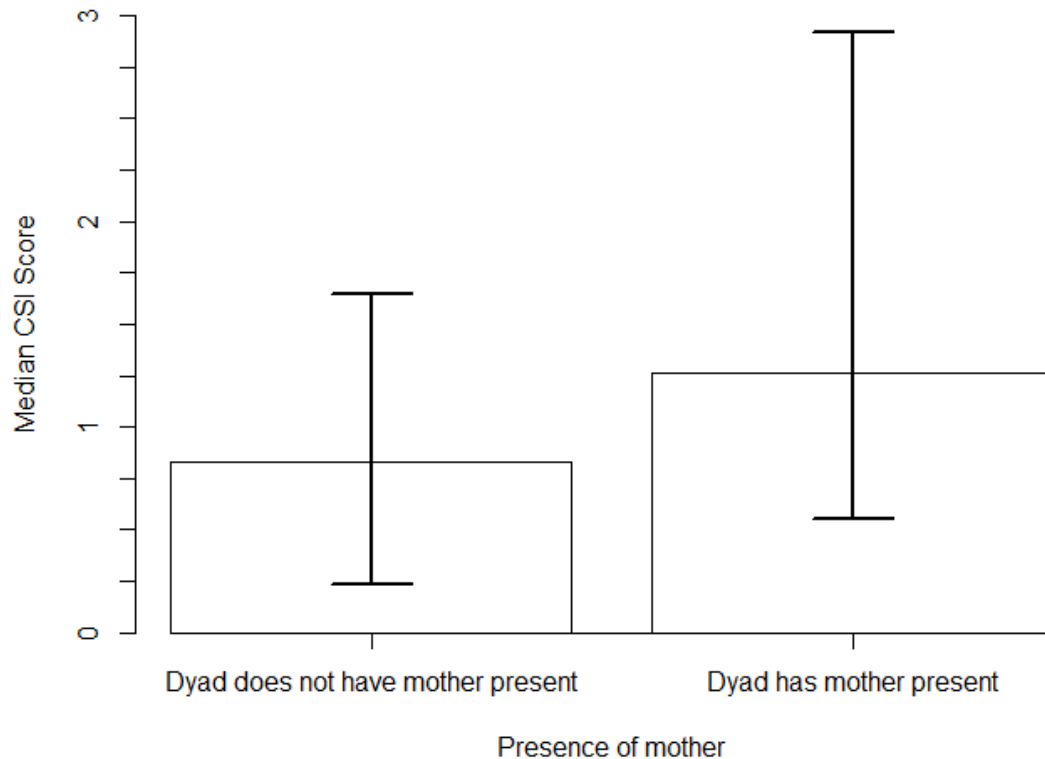


c. Effect of presence of parent on social bond strength between immatures

I first evaluated the effect of having a shared parent in the group on the strength of social bonds between immatures (P2a, P3a, P4a).

Prediction P2a—that immatures with mothers in the social group will sustain stronger social bonds with maternal rather than with paternal half-siblings—was not supported. Among maternal kin, social bond strength (CSI score) did not differ for dyads in which the immatures' mother was present and those in which the mother was absent (present: N=17; absent: N=13; $p=0.29$; Figure 1.3).

Figure 1.3. *Composite Sociality Index (CSI) scores for bonds between maternal half-siblings when their mother is present or absent from the group (present: $N=17$; absent: $N=13$). Error bars were computed by finding 95% confidence intervals for the bootstrapped medians.*

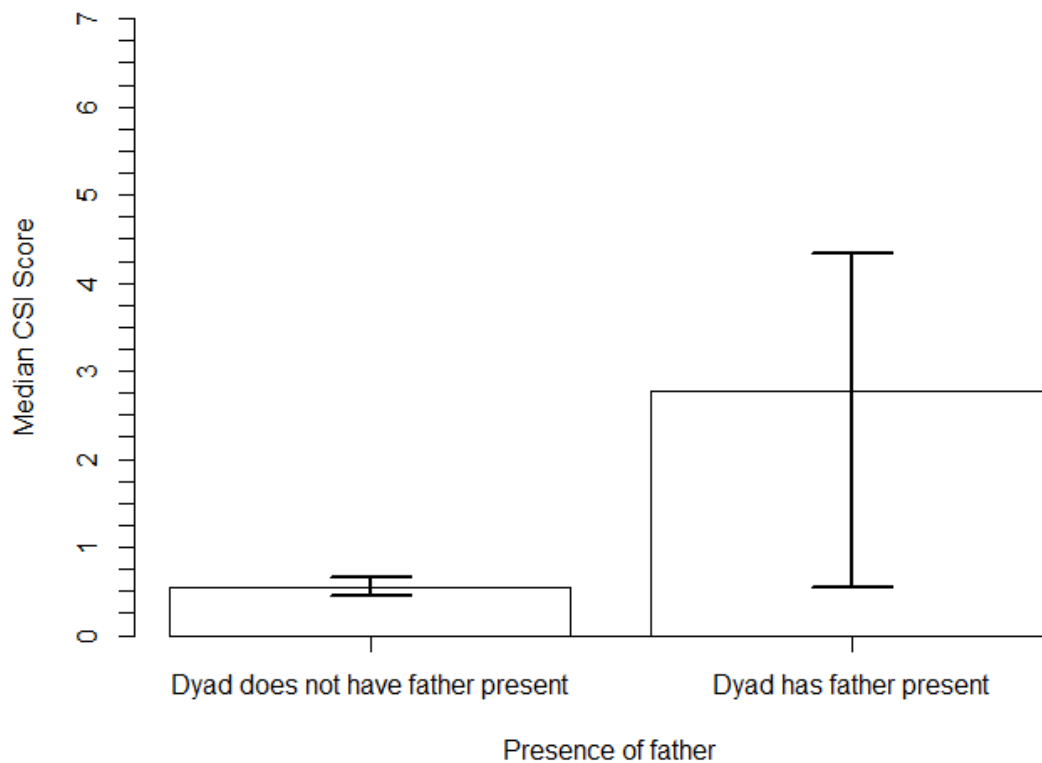


In addition, prediction P3a—that paternal half-siblings will exhibit stronger social bonds when an individual is lacking a mother—was rejected. There was no significant difference in CSI values of paternal half-sib dyads when mothers were present or absent (neither individual has a mother: $N=6$; both individuals have mothers: $N=19$; $p=0.4$).

On the other hand, prediction P4a—that immatures with a father in the group will maintain stronger social bonds with paternal half-siblings compared to those without a father—was supported. CSI scores were significantly different between paternal half-sibs whose father was

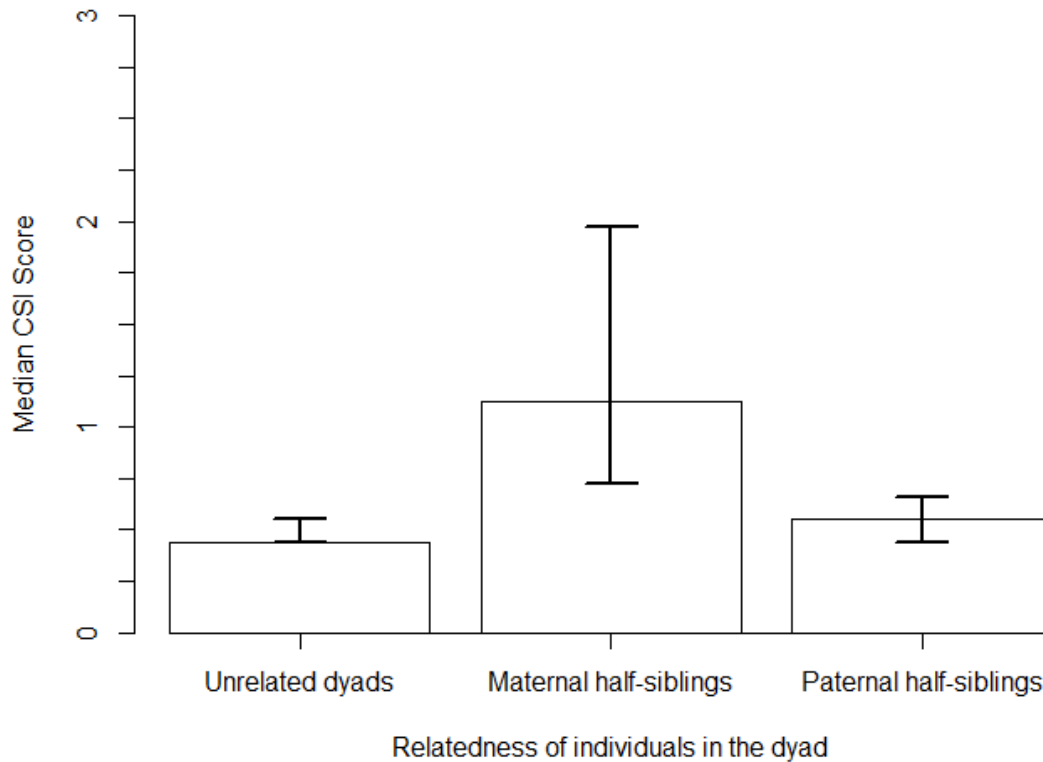
present in the group and half-sibs whose father was absent (present: $N=9$, absent: $N=41$; $p<0.001$; Figure 1.4).

Figure 1.4. *Composite Sociality Index (CSI) scores for bonds between paternal half-siblings when their father is present or absent (present: $N=9$; absent: $N=41$). Error bars were computed by finding 95% confidence intervals for the bootstrapped medians.*



The importance of the presence of the father is illustrated by considering the effect of his absence on the strength of bonds among maternal half siblings and among paternal half-siblings (Figure 1.5). When fathers were absent, the strength of bonds involving paternal half-siblings was significantly different than values for maternal half-siblings (paternal half-siblings without fathers: $N=41$, maternal half-siblings: $N=30$, $p<0.01$), but no different from that characterizing bonds among unrelated individuals (unrelated dyads: $N=668$, $p=0.26$).

Figure 1.5. *Composite Sociality Index (CSI) scores for bonds between different maternal half-siblings (N=30), unrelated dyads (N=668), and paternal half-sibling dyads when fathers were absent (N=41). Error bars were computed by finding 95% confidence intervals for the bootstrapped medians.*



Finally, P4d was supported: social bonds among maternal half-siblings were significantly different when the father was absent compared to when he was present (present: N=10, absent: N=31, $p < 0.001$).

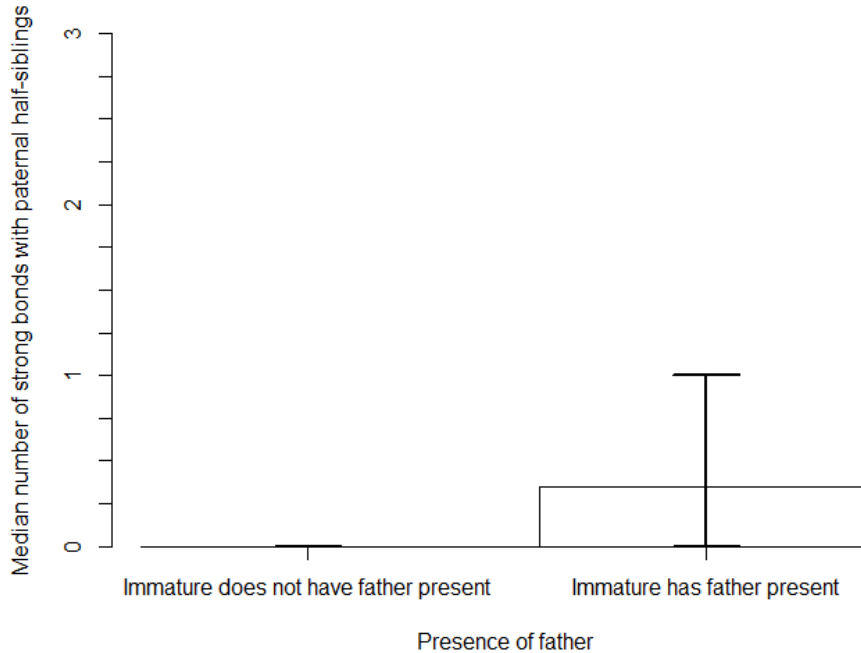
d. The number of strong social bonds an immature maintains varies with the presence of parents

Here I considered the number of strong bonds each focal individual maintained during the course of this study (number of strong bonds involving maternal kin: mean=0.49, S.D.=0.93; number of strong bonds involving paternal kin: mean=0.46, S.D.= 0.81).

Prediction P2b (that immatures with mothers in the group, compared to those without, will maintain more social bonds with maternal half-siblings than with paternal half-siblings) and P3b (that immatures without mothers in the group, compared to those with, will maintain an equal number of strong bonds with both maternal and paternal half-siblings) were both rejected. When comparing immatures with and without mothers in the group, there was no significant difference between the number of strong bonds with maternal and paternal half-siblings ($B=0.41$ ($SE=0.87$), Wald Chi-square=0.22, $p=0.64$).

Prediction P4b—that immatures with fathers in the group, compared to those without, will maintain more strong social bonds with paternal half-sibs—was supported, however. Immatures maintained a larger number of strong bonds with paternal half siblings when their mutual father was present than when he was absent (present: $N=10$, absent: $N=31$, $B=-0.42$ ($SE=0.12$), Wald-Chi-square=11.7, $p<0.001$; see Figure 1.6).

Figure 1.6. *The median number of strong bonds maintained with paternal half-siblings when fathers are present or absent. Error bars were computed by finding 95% confidence intervals for the bootstrapped medians.*



Prediction P4c—that immatures with fathers in the group will maintain fewer bonds with maternal half-sibs—was also supported. An immature without a father in the group maintained more strong bonds with maternal half-siblings (present: $N=10$, absent: $N=31$, $B=0.1$ ($SE=0.15$), Wald-Chi square=0.3, $p<0.05$). Furthermore, for those without a father, the total number of strong bonds maintained with maternal half-siblings increased with maternal half-siblings available ($B=1.48$ [$SE=0.36$], Wald Chi-square=16.62, $p<0.001$).

5. DISCUSSION

The patterns that emerge in this study address the relationship between kin availability and sociality. As reported by Silk et al. (2006b) for adult cercopithecines, immatures in my study sustain social bonds with a small subset of individuals. However, in contrast to my hypotheses and the findings reported for adults by Silk et al. (2006b) and Engh et al. (2006), I found that the presence of mothers does not significantly influence the types of kin that immatures prefer as

targets of social bonding. Alternatively, it is the father's presence that influences social bonds among both paternal and maternal kin in the baboons I studied. Specifically, the bonds between paternal siblings were stronger for those dyads with a shared father in the group than for those without a shared father in the group. Furthermore, immatures with fathers in the group maintained a larger number of strong social bonds with paternal half-siblings and fewer strong social bonds with maternal half-siblings.

These results suggest that fathers facilitate the development of relationships among their young offspring. In contrast to the prediction that individuals will compensate for the loss of mother by strengthening ties with paternal half-siblings, I found instead that immatures without fathers expanded their maternal social network. When fathers are present, immatures appear to invest time and energy into *both* maternal and paternal half-siblings. Specifically, immatures with fathers in the group exhibit stronger bonds with paternal half-siblings and weaker bonds with maternal half-siblings. Therefore, these data suggest that fathers may enable strong social bonds among paternal half-siblings.

The importance of olive baboon fathers in this study may help to explain previously mixed results of studies analyzing affiliation among paternal half-siblings (e.g., Widdig et al. 2001, 2002, 2006; Schülke et al. 2013; Smith et al. 2003; Silk et al. 2006b; Charpentier et al. 2007, 2008, 2012). In one study that did focus solely on immatures (Charpentier et al. 2007, 2012), the presence and influence of a shared father on the social interactions of his offspring was not investigated. This is the first study to examine how fathers influence the types of social bonds that develop among his immature offspring.

Due to the promiscuous nature of the baboon mating system, the limits on paternal kin identification are presumably greater than those affecting maternal relatives. However, maintaining proximity to an adult male confers potential benefits to immatures, such as protection from harassment. Indeed, across various species with similar mating systems, fathers provide such protection for young offspring (e.g., van Schaik and Paul 1996; Palombit et al. 1997; Alberts

1999; Borries et al. 1999; Buchan et al. 2003; Nguyen et al. 2009). A shared interest among multiple immatures in the same adult male may enhance the opportunity for paternal half-siblings to interact (Widdig 2007). Perhaps immatures who prefer to remain near a shared father for individual protective benefits will be more likely to form affiliative relationships with paternal half-siblings (Altmann 1979). On the other hand, in the absence of a shared father, forming strong bonds with paternal half-siblings may be much more difficult. These immatures may solely focus ties with maternal half-siblings, which are able to be readily identified due to live birth and nursing through a shared mother.

If mutual proximity of immatures with a shared father is the factor that facilitates the development of social bonds among paternal half siblings, then a crucial question is whether it is the adult male or the immature who is responsible for this proximity in the first place? While a future analysis will address this question directly, some speculations can be made here. Immatures may be able to identify fathers through “friendships”, which are defined by extended associations between an adult male and a lactating female (Smuts 1985). Friendships may function as a form of paternal investment (van Schaik and Kappeler 1997; Palombit 2000; Moscovice et al. 2010; Cheney et al. 2015). Offspring may then be able to “recognize” one another through a shared association with their mother’s male friend, who is the putative father. In sum, an adult male could be responsible for kin recognition between his offspring

The potential benefits of associating with an adult male may explain why these results do not generally conform with the aforementioned prediction that individuals will compensate for the loss of a mother by strengthening bonds with maternal *and* paternal half-siblings of (Smith et al. 2003; Silk et al. 2006a,b; Engh et al. 2006). Instead, my study corroborates the findings of Charpentier et al. (2012), who also did not observe a correlation between bond strength among immature paternal kin and maternal kin availability. Perhaps young baboons utilize different strategies than their adult counterparts in response to the loss of close maternal kin. There are two possible differences that may explain these alternate strategies.

First, immatures are more likely than adults to have a father in the group. Unfortunately, it is not clear if the adult females in the previously cited studies had access to fathers at any point over their lives. Based on the results presented here, however, the presence of a father may greatly affect the social lives of his offspring. It would therefore be useful to consider the conditions under which a father may be present in a group.

Second, an adult males' presence within a group is dependent partly upon mating opportunities (Alberts and Altmann 1995). Though cercopithecine males typically disperse upon reaching sexual maturity (Pusey and Packer 1987), some adult males may transfer groups again later in life in response to competition with other males (Alberts and Altmann 1995). Alberts and Altmann (1995) have suggested transfer decisions are based on number of breeding males per group, which largely determines the intensity of competition over sexual access to females becomes too high. An alternative strategy to this later transfer for adult males, however, is to remain in a group, and invest in offspring directly or indirectly (Alberts and Altmann 1995; Buchan et al. 2003; Muniz et al. 2006; Widdig 2007).

My results also contradict some researchers' expectations that the loss of a mother will cause individuals to strengthen social bonds with maternal and paternal half-siblings (Silk et al. 2006b; Engh et al. 2006; Smith et al. 2003). Instead, I found that the presence of the father in the social group, but not the mother, was associated with stronger bonds between paternal half-siblings. One reason for the apparent discrepancy may be due to the different age classes of the focal subjects: when faced with the loss of a mother, previous research investigated how social bonds among *adult* females change whereas I examined bonds among *immatures*. The nature of the relationship between an adult female and her mother may be different from one between an immature and its mother, particularly with respect to how they are influenced by other existing relationships. While adult females depend on their mothers primarily to help them maintain alliances with other adults, immatures rely disproportionately heavily on mothers to learn about social and foraging behaviors (Lonsdorf and Ross 2012). Therefore, unlike adult females, the

ability of an immature to compensate for the loss of a mother may not be entirely offset by the development of stronger bonds with half-siblings. Instead, immatures may require the strengthening of bonds with other adult relatives (e.g., aunts) in order to facilitate learning and social development. In other words, because immatures may respond to the loss of a mother differently than adult females, social bonds with paternal half-siblings may also develop in different ways.

An important caveat is that this study does not address directly how individuals may flexibly modify social bonds in response to the loss of preferred social partners. The hypotheses originally put forward by Smith et al. (2003), Silk et al. (2006a,b) and Engh et al. (2006), suggesting that adult individuals compensate for the loss of preferred social partners, could not be directly tested here because this study was not sufficiently longitudinal in nature, in which social behaviors both before and after the loss of a preferred maternal relative (i.e. mothers) could be measured. This study focused solely on the behavioral differences between groups of immatures with and without mothers, which is, however, a rare scenario in fieldwork on wild primates.

A number of studies have reported selective interactions between fathers and offspring among cercopithecine primates (Borries et al. 1999; Buchan et al. 2003; Langos et al. 2013) and fitness benefits associated with fathers or likely fathers (mandrills: Charpentier et al. 2008; chacma baboon: Palombit et al. 1997; Huchard et al. 2012; hanuman langur, *Presbytis entellus*: Borries et al. 1999). While this study provides some of the first data addressing the significance of a father's presence for offspring social behavior, the results presented here corroborate others' findings regarding the adaptive consequences of fathers for offspring survival and reproduction (Charpentier et al. 2008; Huchard et al. 2012). For example, Charpentier et al. (2008) found that a father's presence in a group is associated with an earlier age at which sexual maturity is reached by his offspring; this, in turn, may enhance lifetime reproductive success. Evaluating a possible mechanism behind this phenomenon, Huchard et al. (2012) reported that immatures feed on better quality foods when in proximity to their fathers.

My study builds upon these works by demonstrating the presence of a father in a group facilitates the development of strong social bonds among his offspring. The data reported here also suggests social integration within a matrilocal society may be achieved, not just through bonds with maternal relatives, but also through affiliating with paternal kin. Together, the results highlight the important possibility that even in a social system in which matrilineal kinship powerfully influences group structure and dynamics, paternal kinship may nevertheless form the basis of significant selective forces in social evolution.

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Chapter Two

Mothers and fathers play a role in the development of foraging behaviors in juvenile olive baboons (*Papio hamadryas anubis*)

1. INTRODUCTION

Among mammals, primates exhibit long juvenile periods relative to body size (Harvey and Clutton-Brock 1985; Pereira and Fairbanks 1993; Purvis et al. 2003). During this time, immatures acquire many of the skills necessary for survival and future reproduction (Schulz 1969; Gavan 1982; Pereira and Fairbanks 1993; Lansdorf and Ross 2012), including behaviors commonly used by adult conspecifics to exploit resources successfully (Bock 1995, 2002; Johnson and Bock 2004). Living in social groups, as most anthropoid primates do, is commonly associated with elevated competition over food (Wrangham 1980; van Schaik, 1983), and access to food during development has an important impact on a variety of life-history traits, such as growth rate and age of sexual maturity (Bercovitch and Strum 1993; Alberts and Altmann 2005).

Competition over food influences social behaviors in nonhuman primate groups (see reviews by Chapman et al. 2012 and Schülke and Ostner 2012). The nature of this competition is influenced in part by the quality and distribution of the contested resources (Nicholson 1954; Fretwell 1972; Wrangham 1980; van Schaik 1989; Sterk et al. 1997). Contest competition is more likely to emerge when resources are distributed in discrete patches that potentially facilitate the exclusion of others (van Schaik et al. 1989) or when food sites can be controlled but not easily depleted (Isbell et al. 1998). In contrast, when resources are uniformly dispersed, or large enough that individuals cannot monopolize them efficiently, scramble competition is expected (Parker 1985; Sterk et al. 1997).

Because social interactions often occur while foraging (Goosen 1981; Wang 2000; Sugiura 2007), social factors, such as age and kinship, are expected to affect how individuals forage in these different competitive scenarios (Schülke and Ostner 2012). Juveniles must balance their

efforts between achieving the short-term goal of consuming foods to meet metabolic demands and the long term goal of acquiring the behaviors and knowledge to support effective resource exploitation (Brock 1995, 2002; Johnson and Bock 2004). Both descriptive studies (Altman 1980; Boinski and Fragaszy 1989) and quantitative analyses (Janson and van Schaik 1993; de Ruiter 1986, Johnson and Bock 2004) suggest that foraging rates of juveniles is lower than that of adults (Janson and van Schaik 1993). Juveniles also face more restricted diets. For example, juveniles tend to avoid foods that are tough (van Schaik and Noordwijk 1986) or that require practice in order to extract (e.g., caterpillars with stinging hairs: Boinski and Fragaszy 1989). Consequently, such foods often contribute disproportionately more to adult than juvenile total energy intake (Malenky 1990; Whitehead 1986). A more restricted diet *and* reduced foraging rates are likely to make juveniles particularly sensitive to resource competition, which may account in part for an observed greater percentage of time spent foraging compare to adults (Janson and van Schaik 1993; Altmann 1997).

When feeding is subject to the constraints of intragroup competition or learned competency, close spatial proximity between a juvenile and adult can potentially improve the former's foraging success in at least two ways. First, propinquity to a tolerant adult may beneficially reduce the rate of interruptions from conspecifics, thereby facilitating access to higher quality food resources (Heyes 1994; Schiel and Huber 2006; Huchard et al. 2012). Second, young primates may benefit from observing adults forage. Across a range of species, social learning is critical to the development of foraging behaviors in young animals (Galef and Laland 2005). Immature primates can develop foraging skills through social learning based in part on observing adults feeding nearby (Johnson and Bock 2004; Lonsdorf et al. 2004; Ottoni and Izar 2008; Jaeggi et al. 2010; van de Waal et al. 2013, 2014).

Kin selection theory (Hamilton 1964) predicts that, all else being equal, the close proximity of a feeding juvenile will be tolerated to a greater extent by an adult relative than by an unrelated adult. In partial support of this hypothesis, a number of studies have reported that close maternal

kin will tolerate mutual “co-feeding”—defined as eating in close proximity—more often than do non-kin (McGrew 1975; Silk, 1979; Feistner and Price 1990; Perry and Rose 1994; Belisle and Chapais 2001; Silk et al. 2004).

Much less is known about how paternal kin may impact a young animal’s foraging success, however. Although the promiscuous mating that often characterizes multi-male, multi-female societies would appear to obscure paternity, evidence that fathers affect protect offspring during agonistic disputes with conspecifics (Buchan et al. 2003; Moscovice et al. 2009; Nguyen et al. 2009) or during infanticidal attacks (Borries et al. 1999) raise the possibility of analogous benefits in the context of feeding. In sexually dimorphic species, adult males may be more capable than females of monopolizing patchy food resources (King et al. 2011). Therefore, father-offspring associations have the potential to influence juvenile resource acquisition (Hill 1986; Kaplan et al. 2011). There are very few data directly addressing this question, although Huchard et al. (2012) have reported that father-offspring spatial associations of chacma baboons (*Papio hamadryas ursinus*) are more frequent when juveniles feed in high quality patches.

Here I examine the foraging behavior of juvenile olive baboons (*Papio hamadryas anubis*). Olive baboons live in multi-male, multi-female, matriloca societies in which males typically disperse upon reaching sexual maturity (Pusey and Packer 1987; Palombit 2012). Though some adult males may transfer among groups again later in life, another strategy is to remain in a group, potentially with offspring (Hamilton 1984; Alberts and Altmann 1995; Buchan et al. 2003; Muniz et al. 2006; Widdig 2007). The feeding behavior of young baboons, therefore, may be able be potentially influenced by both maternal and paternal adult relatives.

I predict that juveniles will modify foraging behaviors in response to the immediate social environment and the general acquisition requirements posed by different food types. When consuming foods that are likely associated with contest competition (i.e. patchy resources, such as fruit and seeds), juveniles should feed for longer periods when near a parent than when near an unrelated adult, due to the protection from harassment and displacement a parent may provide.

When consuming foods that require particular behavioral skills (e.g., underground storage organs—USOs—which must be located, extracted, and processed), immatures should feed for longer periods of time when near a parent. This prediction is based upon the expectation that juveniles may enhance their foraging skills through observational learning of co-feeders (see Johnson and Bock 2004). Again, the most tolerant adults are predicted to be close kin, in general, and parents, in particular. Juvenile feeding rates on both types of food are expected to decrease due to the protection provided by proximity to a parent, relative to rates when near an unrelated adult. Finally, I predict that foods that are relatively evenly distributed and abundant (grasses) should not be associated with any changes in the duration or rate of feeding in response to the immediate social environment (i.e., proximity of relatives).

To summarize, I predict:

P1) for foods more likely to engender contest competition, feeding bout duration will be:

(P1a) longer when immatures are feeding near mothers compared to when feeding alone or near other adult females; and (P1b) longer when immatures are feeding near fathers compared to when feeding alone or near other unrelated adult males;

P2) for foods more likely to engender contest competition, the feeding rate will: (P2a) decrease when immatures feed near mothers, compared to when feeding near unrelated adult females or alone, (P2b) decrease when immatures are feeding near fathers, compared to when near unrelated adult males or alone;

P3) for foods requiring extractive skill (OSUs), (P3a) feeding bouts will be longer when immatures are feeding near parents, compared to when feeding alone, (P3b) immatures will exhibit slower feeding rates when near parents compared to when feeding alone or near unrelated adults;

P4) foods that are more evenly distributed, and therefore engendering scramble competition, will not be associated with any differences in feeding bouts or feeding rates when near adults compared to when alone.

2. METHODOLOGY

Study Area:

The study area was located in the Laikipia District of Kenya. Ecologically, the area was the Somali-Maasai Arid Zone (Estes 1991), characterized by dry grassland, scattered thornbush (*Acacia drepanolobium*), small groves of red fever trees (*Acacia xanthophloea*), seasonal watercourses, and several permanent waterholes (see Barton et al. 1993).

The foods commonly eaten by the juvenile baboons in this study are summarized in Table 2.1. The baboons ate a wide variety of foods, including the seed pods, flowers, and gum of acacia trees (*Acacia* spp.), as well as flowers, leaves and fruits of other bushes and herbs (e.g., *Balanites glabra*, *Lycium* spp.). In addition, they often consumed rhizomes, bulbs and roots, most frequently from grass (Smuts 1985, Barton et al. 1993). Finally, they frequently consumed ants, often found in symbiotic association with *A. drepanolobium* (Young et al. 1997).

Subjects:

I collected behavioral data and fecal samples from a group of wild, habituated olive baboons (N=111) that Dr. R. Palombit and colleagues have studied since 2000. Focal subjects were 23 female and 22 immature males. For the analysis, however, six individuals were excluded: three subjects were not clearly genotyped and three others disappeared before sufficient focal data could be collected. The final set of subjects used for analysis, then, comprised 20 male and 19 female immatures.

From a bio-developmental viewpoint, the “juvenile” and “subadult” age classes collectively encapsulate the period that begins with weaning and ends with the attainment of sexual maturity (Pereira and Altmann 1985; Pereira and Fairbanks 1993; Lonsdorf and Ross 2012). None of the subjects were observed to nurse from their mothers or participate in sexual consortships (though, in the case of females, they may have displayed secondary sexual characteristics, such as sexual swellings).

Behavioral Data:

The study took place over an eighteen month period, from April 2010 through June 2011. Daily observational data were collected between 0700 and approximately 1400. Behavioral data were collected via 10-minute focal animal samples (Altmann 1974) during which general activity (e.g., rest, feed [by item], travel) and two categories of social behaviors (affiliative and agonistic) were scored continuously. The identities of nearest neighbors (within 6 meters of the focal individual) were also recorded at two minute intervals during the focal session. Highly conspicuous behaviors and agonistic interactions, such as mounting or chases, were recorded *ad libitum*. I collected approximately 6,800 focal samples over the course of 1,115 hours of observation. For the purposes of this analysis, the behaviors of interest were those of spatial proximity and those related to feeding. Individuals within 6m were considered to be in close spatial proximity.

Measures of Feeding:

Foraging success was defined in two ways: by the duration of the feeding bout and by the feeding rate (Nakagawa 2009). I defined a feeding bout as a discrete unit of time, starting when a focal individual began consuming a food item and ending when it had either stopped consumption of the food for 10 seconds (Altmann 1998) or had moved on to another feeding site or food type (Isbell et al. 1998; Pruetz 2015). Feeding rate was calculated as the number of times an individual's hand delivered food from the food source to the mouth, per minute (Barton et al. 1993; Isbell et al. 1998; Johnson and Bock 2004; Nakagawa 2009). This measured how many items (or feedings) of a particular substrate were consumed per unit of time.

Unlike most adult-oriented definitions of foraging success, which tend to focus on caloric intake, I characterized foraging success in light of the expected need of immature primates to achieve both resource acquisition and opportunities for observational learning. Thus, in this analysis greater foraging success was defined as a slower feeding rate and a longer duration of

feeding time. These combined factors are likely to reflect an immature's ability to "take its time" when feeding while also potentially observing the adult in proximity.

Foods were separated into categories that qualitatively reflected different foraging regimes in terms of intraspecific competition and processing demands. Fruits are generally considered a patchily distributed, defensible resource (Wrangham 1980), and in the study area, fruits are known to promote contest competition among the adult baboon subjects (Moinde 2015). USOs were considered resources whose extraction and processing require skills, which may be learned, partly via socially facilitated observational learning of feeders (Johnson and Bock 2004). Finally, grasses were considered a relatively uniform resource whose exploitation primarily involves scramble competition or, in fact, little competition (Isbell et al. 1998; Moinde 2015).

Table 2.1. *Food types most often consumed by immatures during the study. Foods were categorized into eight "types".*

Food Type	Items within the category
Grasses	Grass shoots/meristems (but not USOs or seeds); <i>Brachiaria lachnantha</i> , <i>Lintonia nutansa</i> , <i>Pennisetum mezianum</i> , <i>P. stramineum</i> , <i>Themeda triandra</i>
Gum/Exudate	Almost always <i>Acacia drepanolobium</i>
Flowers	Primarily from <i>A. drepanolobium</i> , <i>A. xanthophloea</i> , <i>Lycium</i> spp.
Fruits	Primarily <i>Lycium</i> spp., <i>Balanites galabra</i> , <i>Scutia myrtina</i>
Seeds	From trees (primarily <i>A. drepanolobium</i>), grass and feces
Underground Storage Organs	Rhizomes (primarily from grasses), mycorrhizae,
Leaves/Foliage	From <i>Lycium</i> spp., <i>Salvadora persica</i>
Insects	Ants (<i>Crematogaster</i> spp., <i>Tetraponera</i> spp.) in galls of <i>A. drepanolobium</i> (Young et al. 1997)

Genetic Analysis:

See the Methods section in Chapter 1.

Statistical Analysis:

SPSS 21.0 was used for all statistical analyses. To examine how feeding duration and feeding rate vary with spatial proximity (within and beyond 6 meters) to parents, I used a generalized estimating equation (GEE) model. This model was used because it allows for repeated measures (feeding bouts per individual) and the individual was entered as a random

effect. When analyzing bout lengths, feeding duration was the dependent variable and the presence of adults (adult males or adult females, depending on the test) was the independent variable. Maximum-likelihood estimation was used to obtain the parameters of the distribution that resulted in the best fit (i.e., lowest AIC) for both foraging bout length and feeding rate. Based on these results, a gamma distribution was determined to be the best fit and this distribution was assumed in the model.

In these tests, I controlled for the proximity of unrelated adult males and females and for the proximity of a parent, when necessary. In other words, when testing predictions about the effect of proximity of a particular type of adult (e.g. the father) on the foraging behavior of juveniles, I used only feeding bouts in which an individual of that type was the only adult in proximity to the focal animal; focal bouts in which any other adults (e.g. unrelated adult males) were in proximity were excluded. In only one feeding bout for one individual were both parents simultaneously in proximity to the juvenile; this case was excluded from the analysis.

Because processing time is expected to vary with food type (Schülke et al. 2006; Stammati et al. 2008), the analysis of feeding rate was broken down by both food type (Table 2.1) and proximity to adults. The following food classes were excluded from this analysis because they were consumed in less than 5% of the feeding time, or were represented in fewer than 40 feeding bouts: flowers (total bouts: 4) and leaves (total bouts: 36). Here also, a GEE model with repeated measures and gamma distribution was used due to the right skew of the data and the multiple data points of feeding bouts per individual, again with AR-1 structure. However, a binary logistic distribution (e.g., eating a seed vs. not eating a seed per bout) GEE model was used to test the food types themselves against other fixed effects.

3. RESULTS

Frequency of Feeding Bouts:

There were a total of 5,533 feeding bouts involving immatures observed during the study period. Females (N=19) engaged in 2,614 bouts and males (N=20) 2,919 bouts. Across all immatures, 11% of all feeding bouts were near ($\leq 6\text{m}$) the mother of the focal individual and 3% of all bouts were near the father.

Feeding Duration:

Feeding times varied with proximity to adults and food type (Table 2.2). Prediction P1a was supported: for foods promoting contest competition (i.e., fruits), feeding bout duration was longer when immatures fed in proximity to mothers (females, N=20; males, N=25) than when they fed alone (females, N=81; males, N=90) or near other unrelated adult females (females, N=20; males, N=90). Specifically, feeding bouts were, on average, 2.5 times longer when near mothers than when alone and 4 times longer than when near unrelated adult females.

The analogous prediction (P1b) examining the possible effect of paternal propinquity on juvenile foraging bout duration could not be tested because immatures were not recorded consuming fruit in proximity to fathers. This outcome can be partly attributed to the control I used for this analysis, which excluded feeding bouts in which multiple adults were in proximity to the feeding juvenile. In all of the few feeding bouts in which fathers were recorded near feeding focal juveniles, mothers were also simultaneously present.

While I predicted feeding bouts for USOs would be longer when immatures were near their parents (prediction P3), this effect was only seen among same sex parent-offspring dyads. Feeding bouts were shorter when immatures were alone (females, N=180; males, N=144) than when they were near the same sex parent for both juvenile males (N=25) and females (N=20) (prediction P3a) (Table 2.2). Immatures fed 1.5 times longer when foraging on USOs when near a parent of the same sex compared to when feeding alone.

In support of prediction P4, the duration of feeding bouts focused on grasses did not differ when juveniles fed alone (females, N=137; males, N=190) versus near a parent (females near the mother, N=11; females near the father, N=6; males near the mother, N=14; males near the father, N=10) (Table 2.2). Specifically, in all four conditions, the largest difference between eating alone versus eating near a parent was 0.8 seconds, which was not statistically significant.

Table 2.2 *Feeding bout durations compared across the sex category, food type, and proximity (within 6 meters) to parents versus unrelated adults and when foraging alone (no other individuals are within 6 meters). "N/A" refers to cases in which no feeding bouts occurred in one or both comparison groups. See text for details. Results with accompanying asterisks are statistically significant.*

	Fruits	USOs	Grasses
Female Juveniles			
Alone vs. near mother	B=-1.44, Std. error=0.48, Wald=8.82, p<0.005*	B=-5.4, Std. error=0.27, Wald=3.9, p<0.05*	B=-0.04, Std. error=0.43, Wald=0.01, p=0.9
Near mother vs. unrelated adult female	B=3.0, Std. error=0.4, Wald=65.7, p<0.001*	B=-0.3, Std. error=0.51, Wald=0.27, p=0.6	B=-0.1, Std. error=0.46, Wald=0.04, p=0.8
Alone vs. near father	N/A	N/A	B=-0.06, Std. error=0.28, Wald=0.05, p=0.8
Near father vs. unrelated adult male	N/A	N/A	B=-0.34 Std. error=0.38, Wald=0.78, p=0.4

Table 2. Continued

	Fruits	USOs	Grasses
Male Juveniles			
Alone vs. near father	N/A	B=-1.21, Std. error=.22, Wald=30.97, p<0.001*	B=0.86, Std. error=0.64, Wald=1.8, p=0.18
Near father vs. unrelated adult male	N/A	B=1.2, Std. error=0.33, Wald=12.11, p<0.001*	B=-1.3, Std. error=0.7, Wald=3.5, p=0.06
Alone vs. near mother	B=-1.37, Std. error=0.68, Wald=4.07, p<0.05*	B=-0.33, Std. error=0.44, Wald=0.57, p=0.45	B=-0.14, Std. error=0.22, Wald=0.4, p=0.5
Near mother vs. unrelated adult female	B=0.73, Std. error=0.43, Wald=2.9, p<0.05*	B=-0.49, Std. error=0.84, Wald=0.34, p=0.56	B=-0.48, Std. error=0.43, Wald=1.3, p=0.3

Feeding Rate:

The feeding rate on foods expected to generate contest competition (fruits) was lower when immatures fed near the mother compared to when they fed near unrelated adult females (Table 2.3), providing support for prediction P2a. Female juveniles ate at a rate 17 times slower when near mothers compared to when eating alone and 20 times slower when compared to eating near an unrelated adult female. Immature males showed a similar difference in rates: feeding rate with the mother nearby ($\leq 6\text{m}$) was seven times lower than when alone and four times lower than

when near an unrelated female. As mentioned previously, prediction P2b could not be tested because neither males nor females ate fruits exclusively near their fathers.

In contrast to the pattern predicted in P3b, I observed no differences in feeding rates on USOs when near or away from the parent (Table 2.3). This was true for both male and female juveniles.

Finally, foraging on grasses was not associated with any differences in feeding rate in light of parental proximity, supporting prediction P4. As with the results for feeding bouts, there were no statistically significant differences in all four scenarios (each sex feeding near each type of parent).

Table 2.3. *Feeding rates compared across sex category, food types, and proximity (within 6 meters) to parents versus unrelated adults and when foraging alone (no other individuals are within 6 meters). Results with accompanying asterisks are statistically significant.*

	Fruits	USOs	Grasses
Female Juveniles			
Alone vs. near mother	B=2.67, Std. error=0.43, Wald=37.04, p<0.001*	B=-0.42, Std. error=0.61, Wald=0.47, p=0.5	B=-0.23, Std. error=0.27, Wald=0.7, p=0.4
Near mother vs. near unrelated adult female	B=-2.58, Std. error=0.54, Wald=22.99, p<0.001*	B=-0.24, Std. error=0.54, Wald=0.2, p=0.65	B=-0.3, Std. error=0.24, Wald=1.3, p=0.3
Male Juveniles			
Alone vs. near mother	B=1.92, Std. error=0.16, Wald=136.08, p<0.001*	B=-0.46, Std. error=0.81, Wald=0.32, p=0.57	B=0.25, Std. error=0.14, Wald=3.08, p=0.08
Near mother vs. near unrelated adult female	B=-1.2, Std. error=0.18, Wald=44.2, p<0.001*	B=-0.47, Std. error=0.81, Wald=0.34, p=0.56	B=0.08, Std. error=0.11, Wald=0.5, p=0.47
Alone vs. near father	N/A	B=0.18, Std. error=.07, Wald=7.7, p=0.54	B=-0.5, Std. error=0.33, Wald=2.2, p=0.14
Near father vs. near unrelated adult male	N/A	B=-0.1, Std. error=0.17, Wald=0.4, p=0.53	B=0.6, Std. error=0.33, Wald=3.03, p=0.08

4. DISCUSSION

The results of this study augment previous examinations of the development of foraging behaviors in nonhuman primates (e.g., Boinski and Fragasy 1989; Moura and Alonso 2000; Corp and Byrne 2002) by demonstrating the importance of *both* mothers *and* fathers on resource acquisition in juveniles. Perhaps the most salient conclusion derived from these data is that foraging behavior among immatures is affected by proximity to the parent in two conditions: 1) when the cost of contest competition is potentially high; and 2) when the relevant foods are difficult to acquire and therefore likely to involve socially facilitated learning for their exploitation.

First, by maintaining proximity to a parent during foraging, immatures can mitigate the costs of feeding competition. Foods that occur in easily defended patches, such as many types of fruits, are expected to incite contest competition both generally (van Schaik 1989; Sterk et al. 1997) and specifically for the baboon subjects of this study (Moinde 2015). It was consumption of these foods that occurred for longer periods of time when in proximity to a mother. Juveniles may therefore opt to eat near their mothers in order to buffer themselves from harassment during foraging and possibly even from displacement from the food source. Feeding rates, however, increased when juveniles were away from both parents and unrelated adults. One interpretation of this result is that immatures accelerate ingestion of fruit when not near their mothers because they are more vulnerable to competitive exclusion from the resource by conspecifics. In other words, when alone, immatures may “rush” to consume as much as possible in anticipation of being displaced by an adult. When near the mother, however, juveniles may be at lower risk of displacement and may, therefore, take more time to forage at a reduced rate. Due to the sample, I could not test the effects of consuming patchily distributed resources when in proximity to fathers.

Second, juveniles fed on difficult-to-acquire foods for longer periods of time (bouts) when in proximity to a parent of the same sex. A number of researchers have proposed that the

extended period of juvenility in primates can be partially explained by the need to develop effective foraging skills (e.g., Watts 1985; Boinski and Fragaszy 1989; Wiens and Zitzmann 2003; Lonsdorf et al. 2004). Johnson and Bock (2004) have argued that USOs, in particular, require a substantive level of skill in order to locate, harvest, and consume, whereby an individual must work through the challenges of concealment, extraction, and preparation for consumption. They base this argument on data showing that adult chacma baboons (*Papio hamadryas ursinus*) forage more efficiently than juveniles on USOs, which they attribute primarily to differences in cognitive, memory, and fine motor performance. Experience, therefore, appears to be critical when locating and consuming these difficult-to-acquire resources, which suggests that learning may be important.

Results of my study on olive baboons are consistent with this view. When feeding on USOs, feeding rates were the same when juveniles were near or away from parents, which suggests that feeding competition is low or negligible for these foods. Therefore, unlike fruit, the observed longer feeding bout durations for USO's may reflect a different strategy based upon the possible benefits of observational learning. In general, socially facilitated learning is important for the acquisition of information and skills (Pereira and Fairbanks 1993; Hoppitt and Laland 2013). Such observational learning is also sometimes essential for the development of the motor patterns used to acquire food (Galef and Laland 2005). Therefore, sustained foraging near an adult who tolerates its presence may be critically improve an immature's ability to learn how to locate, extract, and consume these concealed and difficult to process resources (Johnson and Bock 2004; Gunst et al. 2008). A parent is a more likely candidate for such a tolerant adult (*sensu* Hamilton 1964).

Although I had predicted immatures will consume difficult-to-acquire foods for longer periods of time (bouts) when near their parents, I only found this effect among same sex parent-offspring dyads. This result suggests a possible sex specific foraging strategy. Juvenile primates, for example, have been reported to prefer interactions with same-sex partners (Ehardt &

Bernstein 1987; Cords et al. 2010; Charpentier et al. 2012; Lonsdorf et al. 2014), which may enhance their ability to learn sex specific social behaviors through observing social interactions while foraging. In chimpanzees, social learning of complex foraging behaviors, such as termite fishing, is driven by sex specific interactions (Lonsdorf 2005). Here, a possible interpretation is that juveniles are attempting to learn both foraging and social behaviors from adults of the same sex. The component parts of social learning and foraging behaviors, however, were not measured here.

Alternatively, differences in dominance status of males and females may play a role in these apparent sex specific foraging behaviors of juveniles. In matrilineal societies such as those of the olive baboon, all adult females typically rank below all adult males in the dominance hierarchy. Among young cercopithecines, immature males are better able than females to approach and maintain proximity with adult males (Nakamichi 1989, 1996; Lonsdorf et al. 2014). Thus, although immatures of both sexes may benefit from the company of fathers (due to the enhanced protection that they may acquire), perhaps young males are better able to exploit this advantage. In other words, male juveniles may be seeking this form of protection from related adult males who are more likely to tolerate their presence, while female juveniles are unable to overcome such rank restrictions.

By confirming that fathers influence offspring foraging behavior, this study builds upon other research that suggests adaptive benefits of fathers (Charpentier et al. 2008; Huchard et al. 2012). Charpentier et al. (2008) found that the presence of fathers was associated with the accelerated maturation of offspring, indicating an increase in lifetime reproductive success. Huchard et al. (2012) argue that the proximate mechanism underlying this phenomenon is likely to be paternal enhancement of offspring access to high quality food patches.

Several caveats must be considered when interpreting these results. For instance, strategies other than foraging and social learning may be utilized by immatures. Predation risk, in particular, has been proposed to influence juvenile behavior (Fitchel 2012). The shorter feeding

bouts and high feeding rates experienced by juveniles when away from mothers could reflect an anti-predation tactic, as they are “rushing” through feeding in situations in which a potentially protective mother is nearby.

It should also be noted that the dominance rank of juveniles may play a role in their foraging behavior. This was not measured in this study for two reasons. First, the process of rank acquisition in juveniles is not entirely clear. For many female Old World monkeys, maternal kin come to occupy adjacent ranks in the hierarchy because dominance status is “inherited,” i.e., daughters typically ascend to ranks immediately below their mothers and younger sisters (Cheney 1977; Datta 1983, Paul and Kuester 1987; Chapais 1992; Chapais and Gauthier 1993). For juvenile of pre-reproductive age, the support of maternal kin is critical to maintain these ranks (Pereira 1988; Fairbanks 2002; Range 2006). Juveniles may rank below all other adults, even those in lower-ranking matriline (Berman 1982), and rank may play a small role within juvenile-juvenile interactions (Pereira 1988; Cords et al. 2010). The period of juvenility may provide the opportunity for these immatures to acquire the necessary social skills to attain the ranks below their mothers (Lonsdorf and Ross 2012). Therefore, this period of development may not be associated with the stable, linear ranks typically found among the adults.

Second, the data collection phase of this project began immediately following an unexpected event. During a relatively short period (approximately 2 months), twelve adult females, five subadult females, and five adult males disappeared from our study group. Several lines of evidence implicate leopard predation as the likely cause (Danish, Lynch, Moinde, and Palombit *in prep*). Following this event, many consistent and noticeable changes in female rank occurred (Lynch et al. *in prep*). While these data are currently under analysis, the disruption to the hierarchy was observed throughout the majority of the duration of this study. This relative instability of the dominance hierarchy may have influenced the role of rank on juvenile foraging behavior.

Finally, while I evaluated the foraging patterns of juveniles in response to propinquity of adults, I did not examine the possible effects of variables such as the overall availability or quality of food types. A chemical analysis assessing the effects of parental presence on energetic intake of juveniles would be a useful expansion of this study. Moreover, I was not able to include data regarding the quality and size of food patches. Future studies would benefit from using more detailed information of the spatial placement and nutrient content of food sources to better evaluate the impact of kin on foraging.

In summary, *both* mothers *and* fathers were associated with aspects of juvenile feeding related to foraging success among the juvenile offspring. For immatures, feeding near parents may alleviate some of the costs of contest competition and increase opportunities for socially facilitated learning. This study expands upon our understanding of juvenile feeding behaviors, while highlighting the importance of maternal and paternal kin in a matrilocal society.

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CHAPTER 3

Paternal and maternal half-siblings provide short-term feeding benefits in juvenile olive baboons (*Papio hamadryas anubis*)

1. INTRODUCTION

A fundamental assumption underlying models of primate behavior is that kin selection affects the evolution of social interactions (Gouzoules and Gouzoules 1987; Chapais 2001; Silk 1987, 2002; Langergraber 2012). Individuals are expected to preferentially direct affiliative and cooperative behaviors towards kin, thereby increasing their inclusive fitness. My study sought to broaden our understanding of kin selection by exploring a relatedness category that is often neglected: *paternal* kinship.

On a functional level, kin selection theory (Hamilton 1964) does not discriminate between maternal and paternal relatives. For example, the coefficient of relatedness (r) of 0.25 for half siblings could represent a shared mother *or* father. And yet, our understanding of kinship in primates is focused heavily on maternal kin for at least two reasons. First, maternal relatedness is easily assigned by researchers through long-term observations of births. Second, many monkey groups are organized around matrilineal systems of philopatric females (Gouzoules and Gouzoules 1987). A number of studies of these societies have shown that maternal kinship is associated with affiliative interactions, such as grooming, proximity maintenance, and protective intervention (e.g. macaques, *Macaca* spp.: Chapais 1983; Bernstein and Ehardt 1986; Kuester et al. 1994; Chapais et al. 1997; 2001; baboons, *Papio* spp.: Hausfater et al. 1982; Cheney 1978; Altman 1980; Silk et al. 2004, 2006, 2010a). It has also been shown that social behavior, in general, can affect resource acquisition (Altmann et al. 1988; van Schaik 1989; Barton and Whiten 1993; Hauser 1993; Sterck et al. 1997; Altmann 1998; Koenig 2000; Altmann and Alberts 2003, 2005) and, ultimately, lifetime reproductive success (Cheney et al. 1986; Silk et al. 2003, 2012; Charpentier et al. 2012).

Much less is known about the possible significance of paternal kinship primarily because genetic analysis is needed to assign paternity. Although it may not be obvious in matrilocal societies, several forms of paternal kinship are also potentially present. For example, if male reproductive skew is high, age cohorts of youngsters are likely to include many paternal half-siblings (Altmann 1979a). Also, if male tenure lasts for more than one breeding season, individuals born in the same group may share both a mother and a father (i.e., they will be full siblings). Therefore, matrilocal residents, specifically adult females and immatures, may co-reside with both *paternal* half-siblings and full-siblings. Furthermore, fathers may be present in an individual's social group throughout development and into early adulthood. With recent technological advancements, we are now able to extend our understanding of the evolutionary importance of kinship in matrilocal species to paternal relatives.

To date, only a few studies have investigated the nature of affiliative behavior among *paternal* kin in matrilocal societies (rhesus macaques, *M. mulatta*: Widdig et al. 2001, 2002, 2006; yellow baboons, *P. h. cynocephalus*: Alberts et al. 1999; Buchan et al. 2003; Smith et al. 2003; Silk et al. 2006, mandrills, *Mandrillus sphinx*: Charpentier et al. 2007, 2008, 2012; chacma baboons, *P. h. ursinus*: Nguyen et al. 2009; Huchard et al. 2012). While these studies demonstrate that individuals can preferentially associate with paternal kin, more work must be done to better understand the adaptive significance of these relationships.

With long-lived animals such as primates, proxies for reproductive success must be found in order to estimate how social behaviors affect long-term fitness outcomes (Cheney et al. 1986; Silk et al. 2003, 2012; Charpentier et al. 2012). In principle, success at foraging may be conceptualized as “fitness units” (but see Altmann 1998 for a quantitative assessment). Therefore, kin selection predicts that an individual should forage in a manner that is beneficial not only for itself, but also for close relatives with which it interacts.

Researchers often interpret co-feeding on limited resource patches that can sustain only a few individuals at any given time as reflecting social tolerance of others in a context otherwise

promoting contest competition (van Schaik et al. 1989; Isbell et al. 1998; Belisle and Chapais 2001). Contest competition arises when resources are distributed in discrete patches, so that individuals can effectively exclude others from the source (Fretwell 1972; van Schaik et al. 1989) such as with fruits commonly (van Schaik 1989; Sterck et al. 1997), or when food sites can be controlled but not easily depleted (Isbell et al. 1998). In such an ecological scenario permitting feeding exclusion, tolerance from others becomes a potentially important means of food acquisition. For example, immature olive baboons are able to sustain longer periods of uninterrupted feeding when they are close proximity to their mother than when away from her (see Chapter 3). This “tolerated co-feeding” is sometimes presumed to be a passive form of altruistic food sharing, which raises the possibility that it’s evolution may be governed in part by kin selection (Belisle and Chapais 2001). Accordingly, some studies have suggested that tolerated co-feeding occurs most frequently among closely related maternal relatives (Belisle and Chapais 2001) and may beneficially impact reproductive parameters (Kapsalis 2004), such as age of sexual maturity (Charpentier et al. 2008; Huchard et al. 2012).

While there are relatively ample data on kin-directed behaviors among adult nonhuman primates, the lives of subadults and juveniles still remain relatively unexplored (Walters 1987; Pereira & Fairbanks 1993; Cords et al. 2010; Lonsdorf & Ross 2012). It is true that are “practical reasons” (Pereira and Fairbanks 1993: vii) for the “paucity of data” addressing juvenile feeding and social behavior among siblings (Lonsdorf and Ross 2012), such as a greater tendency to be out of sight and harder to identify compared to adults. Nevertheless, it is clear that a greater understanding of the biology of this maturational period of the life will broaden our understanding of the ontogeny of both feeding and kin-directed social behaviors of primates in particular, and mammals in general.

Juvenile primates are an excellent model for testing theories regarding resource acquisition. Compared to other mammals, primates experience longer periods of dependency before reaching sexual maturity (Isler and van Schaik 2012). During this time, they acquire many of the skills

necessary for solving the problems of survival and future reproduction, such as foraging for food, avoiding predators, and navigating complex social environments (Lansdorf and Ross 2012). In the context of feeding, the limited experience of juveniles means that their dietary diversity (van Schaik and Noordwijk 1986; Janson and Boinski 1992; Boinski and Frigaszy 1989) and overall foraging success are typically lower compared to adults (Bock 1995, 2002). Part of this outcome may also be due to juveniles' greater susceptibility to within-group feeding competition. One possible solution for immatures to improve foraging success and reduce the costs of contest competition is to acquire the assistance of kin. That is, juveniles may benefit from foraging near relatives in at least two ways: by reducing interruptions from rivals (Heyes 1994; Schiel and Huber 2006; Huchard et al. 2012) and by learning foraging skills through the observation of nearby kin who harvest, process, and consume foods (Johnson and Bock 2004; Ottoni and Izar 2008). In this scenario, juveniles are expected to have longer feeding bouts when near relatives (due to fewer interruptions) and slower feeding rates (due to less competition and threats of being displaced).

This study evaluates the foraging behaviors of immature maternal and paternal half-siblings in wild olive baboons (*Papio hamadryas anubis*). The social system of these primates provides an excellent model to explore behaviors among maternal *and* paternal kin. In this matrilineal, multimale-multifemale society, where male reproductive skew is relatively high, age cohorts of offspring are expected to comprise many paternal kin in the form of half-siblings or full-siblings or both (Altmann 1979; Widdig 2007). In addition, adult males may remain within a social group for a variable periods of time, depending upon mating opportunities, age, and past reproduction (Alberts and Altmann 1995). Though cercopithecine males typically disperse upon reaching sexual maturity (Pusey and Packer 1987), some adult males may transfer among groups again later in life in response to intrasexual competition for sexual access to females relative to mating opportunities available in other groups (Alberts and Altmann 1995). An alternative reproductive strategy based more on past mating outcomes than on future mating opportunities is for adult

males to remain in a group, potentially with their offspring, whose survival and success they can influence (Alberts and Altmann 1995; Buchan et al. 2003; Muniz et al. 2006; Widdig 2007).

From this framework I derive and test predictions concerning the foraging of maternal and paternal half-siblings:

P1) When feeding on defensible, discrete resources that have the potential engender contest competition young baboons will experience longer feeding bouts and slower feeding rates when in proximity to a (P1a) maternal sibling, or a (P1b) paternal sibling compared to when feeding near an unrelated individual or alone.

Next, due to a rare demographic event, I was able to compare the foraging behaviors of two sets of immatures: those with mothers and/or fathers in the group and those lacking one or both parents. Chapter 1 previously analyzed how parents influence social bonds among young offspring and Chapter 2 analyzed how parents alter the feeding behaviors of their offspring. In a post-hoc analysis, I extended these findings to examine how half-siblings influence foraging behaviors, with respect to the presence and absence of a shared parent in the social group. Using the same rationale presented earlier, I predict that the stronger social bonds described in Chapter 1 will translate into foraging benefits expressed through longer feeding bouts. For maternal half-siblings, a mother's residency was not found to have any effect on her offspring's social bonds. Therefore, I predict that:

P2) When feeding on defensible, discrete resources that have the potential engender contest competition, maternal half-siblings with mothers present in the group will experience feeding bouts similar to maternal half-siblings without mothers present in the group.

For paternal half-siblings, a father's residency was found to enhance social bonds among his offspring (Chapter 1). Accordingly, I predict that:

P3) When feeding on defendable, discrete resources that have the potential engender contest competition paternal half-siblings with fathers present in the group will experience longer feeding bouts than those without fathers in the group.

2. METHODS

Study Area:

The site was located in the Laikipia District of central Kenya. The vegetation is characterized as the Somali-Maasai Arid Zone (Estes 1991), comprising dry grassland, scattered thornbush (*Acacia drepanolobium*), small groves of red fever trees (*Acacia xanthophloea*), seasonal watercourses, and several permanent waterholes (see Barton et al. 1993). Rainfall ranges from 400 mm in northern Laikipia to 1200 mm in the south (Butynski and de Jong 2014).

Baboons eat a wide variety of local foods, including the pods, flowers, and gum from the acacia trees (*Acacia* spp.), and flowers, leaves and fruits of other bushes and herbs (e.g., *Balanites glabra*, *Lycium* spp.). They also often consume rhizomes, bulbs, and roots (Smuts 1985; Barton et al. 1993). In addition, many grass species are used as food sources (the dominant grasses being *Brachiaria lachnantha*, *Lintonia nutansa*, *Pennisetum mezianum*, *P. stramineum*, and *Themeda triandra*). Finally, the olive baboons frequently consume ants (*Crematogaster* spp. and *Tetraponera* spp.) found in symbiotic association with *A. drepanolobium* (Young et al. 1997). The foods eaten by the juvenile baboon subjects in this study are summarized in Table 1 of Chapter 3 (see above).

Subjects:

From April 2010 through June 2011, I collected data on a group of habituated olive baboons (N=111) that Dr. R. Palombit and colleagues have studied since 2000.

Juveniles and subadults are typically defined as individuals that belong to an age period beginning with weaning and ending with attainment of sexual maturity (Pereira and Altmann 1985; Pereira and Fairbanks 1993; Lonsdorf and Ross 2012). Accordingly, none of the subjects

classified as “juveniles” in this study were observed to nurse from their mothers, and all of the subadults were prereproductive (i.e., had not yet engaged in a sexual consortship [sensu Hausfater 1975], but, in the case of females, might display sexual swellings). For the purposes of simplicity, both age groups will be referred to henceforth as “immatures” or “juveniles”.

Throughout the duration of my study, there were 45 subadults and juveniles who met these criteria and were subjects of this study. Three of these individuals were subsequently excluded from the analysis due to inconclusive genotyping, and an additional three juveniles were excluded due to either their disappearance or their maturing into adults before sufficient observations could be made. The final subject group for the analysis comprised 19 females and 20 males

Behavioral Data:

Behavioral data and fecal samples were collected from April 2010 through June 2011. Observational data were typically collected between 0700 and approximately 1400 hours via 10-minute focal animal samples (Altmann 1974). During each focal sample, all transitions in activity (e.g., rest, feed [by food item], travel) and behaviors belonging to two general social categories (affiliative and agonistic) were scored continuously. I additionally collected spatial proximity in two ways: 1) all movements (approaches and withdrawals) within 2m toward or from the focal individual were continuously recorded during each focal session; and 2) at two minute intervals, the focal individual’s “nearest neighbors”—defined as all conspecifics within 6m—were recorded instantaneously. In total, I collected approximately 6,800 focal samples over the course of 1,115 hours of observation of 39 juveniles.

Measures of Feeding:

To measure tolerated co-feeding, I compared the length of “feeding bouts”. A feeding bout was defined as a discrete unit of time, starting when an individual begins consumption of a food and ending when an individual ends consumption of this food for either 10 seconds (Altmann

1998) or when the individual moves on to another discrete feeding site of the same or different food type, e.g., another individual tree (Isbell et al. 1998; Pruetz 2009).

Feeding rate was calculated as the number of times an individual's hand delivered food from its originating natural source to the mouth, per minute (Barton et al. 1993; Isbell et al. 1998; Johnson and Bock 2004; Nakagawa 2009).

Only feeding bouts that involved patchily distributed or defensible food items were considered in this analysis because of the relevance of contest competition for the predictions (see above). The following taxa were included in this analysis and defined as patchily distributed fruits: *Lycium* spp., *Balanites* spp., *Scutia myrtina*, *Carissa edulis*, *Capparis* spp., *Solanum icanum*, *Tribulus terrestris*.

Predation-based Demographic Event:

An unusual and unanticipated opportunity to analyze kin-directed social behaviors occurred early in the study. Over an approximately 3-month period, twelve adult females, five subadult females, and five adult males disappeared from the study group. Several lines of evidence suggested leopard activity as the cause: new claw marks on the baboon sleep trees, the physical remains of dead baboons near these trees, and nocturnal leopard vocalizations (Danish et al., *in prep*). As a result, approximately half of the focal subjects lost their mother from the group. Although less unusual than the loss of mothers at such a young age, the group also lost five adult males (three of which had offspring in the group, but see “Types of dyads and individuals used in the analysis”). The change in group composition that resulted from these disappearances was effectively a “natural experiment” and allowed for the opportunity to compare the social behaviors of juveniles with and without mothers and fathers.

Genetic Analysis:

See “Genetic Analysis” in Chapter 1.

Types of dyads and individuals used in the analysis:

Of the 39 focal individuals, 33 had at least one maternal half-sibling, 34 had at least one paternal half-sibling, and three had at least one full sibling. Because individuals related as full siblings constituted too small of a sample (N=4) the analysis here focuses entirely on half-siblings. Dyads in which individuals did not share a mother, father, or both were categorized as “unrelated”.

Not all parents were present in the group during the entire duration of this study. The mothers of 18 of the focal individuals were not in the group during part or all of the study period (N=10). Six of these females (the mothers of nine immatures) were absent when data collection commenced. Another four females (the mothers of nine immatures) disappeared during the predation event shortly after the study began. These mothers were therefore categorized as “absent” in the analysis.

In addition, the fathers of 31 focal individuals were not present in the group during part or all of the study period. Eleven males (the fathers of twenty-two immatures) were already missing from the study group when data collection commenced. Another three males (the fathers of nine immatures) disappeared during the predation event. These adult males were categorized as “absent”.

The other adult males and females who were in the group with their immature offspring were therefore categorized as “present” in the analysis.

Statistical Analyses:

Statistical tests utilized SPSS 21.0. To examine feeding, I used a generalized estimating equation (GEE) model with a gamma log link distribution, AR-1 covariance structure (because bouts for the same individual are assumed to co-vary). A GEE was used because the data included repeated measures (feeding bouts per individual); a gamma log link distribution was assumed because the data were heavily right skewed (this distribution generated the lowest AIC score). A pairwise comparison of this model was used to evaluate differences between dyad types

(e.g., feeding near paternal half-siblings vs. feeding near unrelated individuals). Depending upon the prediction, either feeding rate or bout duration was the dependent variable, and proximity to a juvenile (scored as maternal half-sibling, paternal half-sibling, or unrelated) was the independent variable. In all tests reported here, I controlled for the presence of adults (i.e., all feeding bouts where an adult was within 6 meters were excluded from the analysis) due to possible confounding effects on feeding behavior (Chapais 1988; Chapais et al. 1997; Chapais et al. 2001). Also, when comparing co-feeding near different types of kin, only bouts in which that particular kin type was present were used (i.e., feeding bouts near a maternal half-sibling were compared to those where the only individual co-feeding was nonkin).

3. RESULTS

Feeding behavior in proximity to related versus unrelated immatures:

Prediction P1a was supported for the feeding of juveniles near maternal half-sibling versus unrelated individuals. First, feeding bout durations were approximately 80% longer when immatures were in proximity to a maternal half-sibling (N=19), compared to when they fed near an unrelated individual (N=22) ($B=0.63$ ($SE=0.27$), Wald Chi-square=5.6, $p<0.05$) (Figure 3.1). Second, feeding rates were 18% slower when juveniles were in proximity to a maternal half-sibling as compared to an unrelated juvenile ($B=-0.17$ ($SE=0.07$), Wald-Chi-square=5.5, $p<0.05$) (Figure 3.2).

Both measures of Prediction P1b were also supported for paternal half-sibling dyads. When juveniles ate near a paternal half-sib (N=16), feeding bouts were also approximately twice as long compared to when they fed in proximity to an unrelated juvenile ($B=0.69$ ($SE=0.28$), Wald Chi-square=6.1, $p<0.05$) (Figure 3.1). Juveniles also ate 19% slower when in proximity to a paternal half-sibling compared to an unrelated immature (Figure 3.2).

Feeding behavior in proximity to related immatures versus when alone:

In support of predictions P1a and P1b, feeding bouts were longer when near maternal ($B=0.63$ ($SE=0.12$), Wald Chi-square=27.8, $p<0.001$) and paternal ($B=0.69$ ($SE=0.16$), Wald Chi-square=17.5, $p<0.001$) half-siblings compared to when eating alone (Figure 3.1). Feeding rates were also slower by 27% and 31% when eating near maternal ($B=-0.18$ ($SE=0.07$), Wald Chi-square=6.4, $p<0.05$) and paternal ($B=-0.22$ ($SE=0.1$), Wald Chi-square=4.3, $p<0.5$) half siblings, respectively, compared to when eating alone (Figure 3.2).

Figure 3.1. The mean feeding bout duration when in proximity to different types of individuals and when alone. Standard error bars represent 95% confidence intervals.

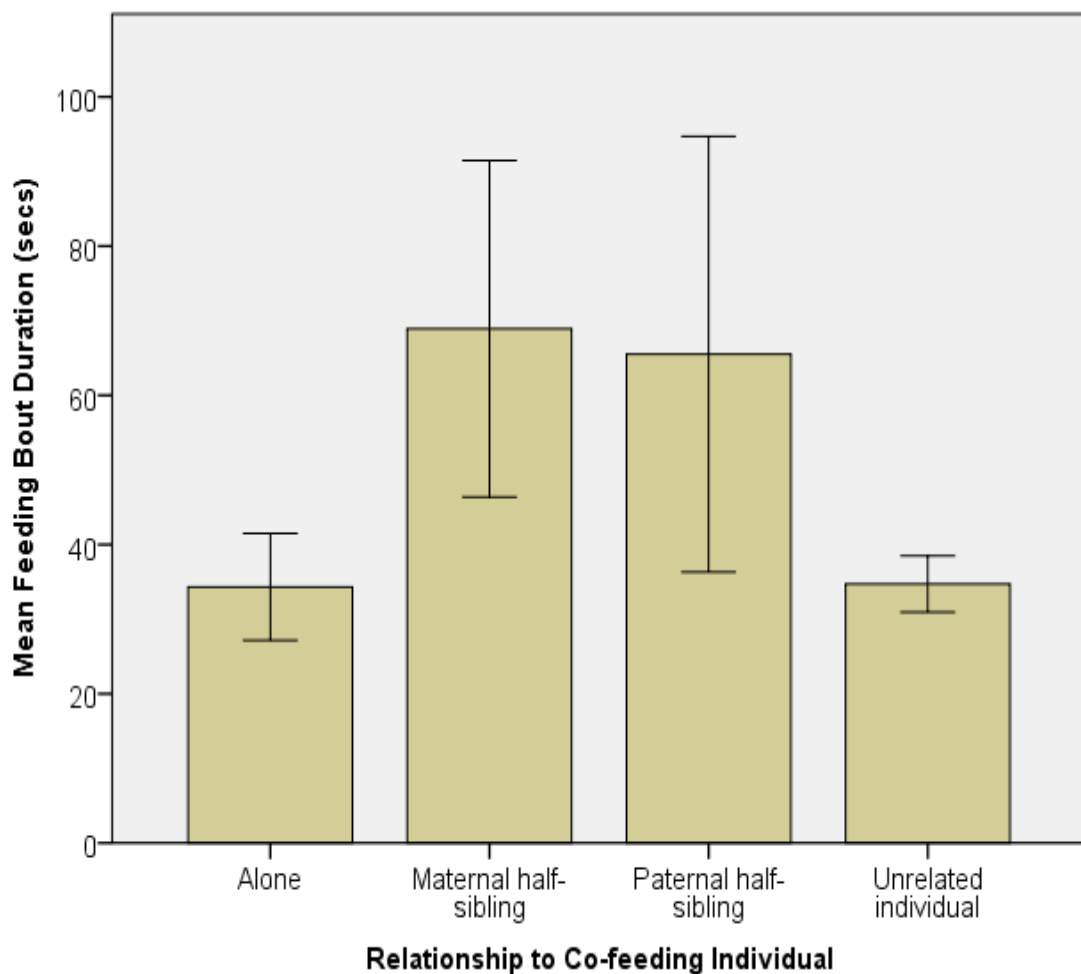
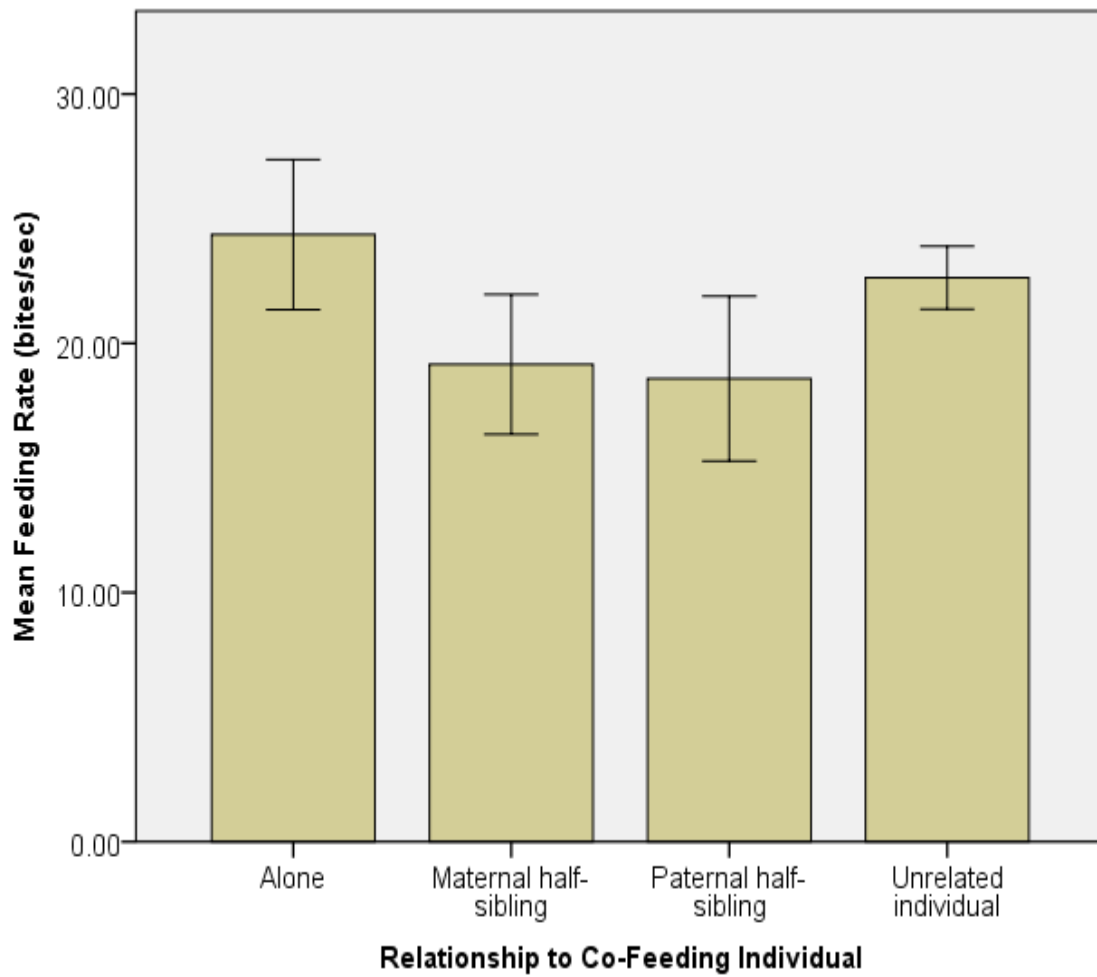


Figure 3.2. The mean feeding rate when in proximity to different types of individuals and when alone. Standard error bars represent 95% confidence intervals.



Feeding behavior in light of the residency of a shared parent in the group:

Individuals without resident mothers in the group (N=17) fed almost four times as long when eating near maternal half-siblings compared to those whose mother resided in the group (N=13) ($B=1.4$ ($SE=0.36$), Wald Chi-square=14.5 $p<0.001$). This result contrasts sharply with the prediction (P2) that the feeding of maternal half-siblings would not differ significantly with respect to maternal presence in the group. Finally, the feeding durations among paternal half-

siblings without resident fathers in the social group (N=41) were approximately four times shorter than those with fathers (N=9) ($B=-1.36$ ($SE=0.45$), Wald Chi-square=9.2, $p<0.01$), which provides support for P3.

4. DISCUSSION

This study provides evidence that both paternal and maternal relatives enhance the foraging outcomes of immature olive baboons. These results add to previous evidence that maternal half-siblings experience significantly longer feeding bouts and slower feeding rates when in proximity to one another than when near an unrelated individual (McGrew 1975; Silk 1979; Feistner and Price 1990; Perry and Rose 1994; Belisle and Chapais 2001; Silk et al. 2004). This study additionally reports a similar pattern among juvenile paternal half-siblings. Furthermore, residency of a shared parent was found to mediate these effects: when a shared father was in the social group, paternal siblings experienced longer feeding bouts when in proximity to one another compared to those dyads whose father was absent. Maternal half-siblings, on the other hand, exhibited longer feeding bouts when their mother was absent from the social group, compared to juvenile dyads whose mother was resident.

Kin selection theory (Hamilton 1964) predicts that, all else being equal, relatives are more likely than nonkin to tolerate the presence of one another, not just in general but when feeding on limited resources promoting contest competition in particular. This enhanced tolerance of kin may provide short term fitness benefits by increasing foraging opportunities. Previous research has shown that both maternal relatives (Imakawa 1988; Belisle and Chapais 2001; Ueno 2005; Clarke 2010) and fathers (Johnson and Bock 2004; Huchard et al. 2012) are associated with enhanced foraging opportunities for young baboons and offspring, respectively. Here I show that juveniles are able to feed for longer periods of time, and at a slower pace, when near a half-sibling, suggesting greater tolerance which, in turn, may lead to fitness benefits.

Although tolerated co-feeding has been reported among maternally related *adult* females in similar species (e.g., Japanese macaques, *Macaca fuscata*: Belisle and Chapais 2001), this

study is novel in its exploration of feeding behaviors exclusively among *immatures*. The juvenile period is typically characterized by high vulnerability due to increased predation risk, lack of experience, reduced nutritional condition, and reduced maternal involvement compared to the infant period (Janson and van Schaik 1993). The behavior of post-weaned, pre-reproductive individuals is therefore likely to reflect adaptations to these contingencies of safety and nutrition (Berman 2004). While many researchers have noted consistent social interactions among immature relatives (reviewed by Nicholson 1987), few have examined how these relationships translate into foraging success (Lonsdorf and Ross 2012). Infant rhesus macaques raised with siblings were found to become independent from their mothers at an earlier age and develop a more complete behavioral repertoire than those reared without siblings (Suomi 1982; Berman 1982). Brent et al. (1997) similarly showed that young chimpanzees with siblings also experienced accelerated independence from their mothers compared to those without siblings. Partly because the foods I examined are subject to contest competition in this troop of baboons (Moinde 2015) and of relatively high nutritional value (Barton et al. 1996), variation in tolerated co-feeding on these resources may have significant long term adaptive consequences on survival and aspects of reproductive success, such as maturation rate (Altmann and Alberts 2003; Johnson 2003; Wasser et al. 2004).

In the social domain, variation in interactions among siblings has been correlated with fitness outcomes in haplorrhines (see review by Silk 2012). For example, in species where females are philopatric and males disperse, young females generally show social preferences for matrilineal kin, and these relationships last into adulthood (Pereira and Fairbanks 1993; de Waal 1996; Silk et al. 2006). Cohesive social integration among females enhances both lifetime reproductive success (Silk et al. 2003, 2009) and lifespan (Silk et al. 2010b; Archie et al. 2014).

It should be noted, however, that the data presented here on olive baboons suggests that any positive developmental or adaptive effect of tolerance among siblings is potentially mitigated by the presence or absence in the group of the parent of the siblings. A father's residency was

associated with longer feeding bouts among paternal half-siblings compared to those without fathers in the social group. Interestingly, the opposite pattern was found among maternal half-siblings: for those without a mother present in the group, feeding bouts were longer compared to half-siblings with a mother in the group. One interpretation of these ostensibly contrasting results is that juvenile strategies differ across kin types and contingency (i.e., social bonding versus foraging). While the loss of a mother has no significant effect on social bonds among young maternal half-siblings (Chapter 1), juveniles without mothers in the social group appear to spend more time foraging near maternal half-siblings. As suggested in Chapter 1, immatures may compensate for the absence of a mother by preferentially strengthening bonds with adult kin, such as maternal aunts, rather than similarly aged half-siblings. The same situation of maternal absence, however, appears to promote a strategy of increasing proximity to half siblings during foraging, possibly to ameliorate the costs of losing the mother as foraging partner. Immatures may also compensate for this loss by feeding longer when near older maternal kin and this possibility will be examined in a future analysis.

A different phenomenon may explain the patterns observed among paternal half-siblings. In Chapter 1, I showed that among paternal siblings, bond strength was higher for juveniles whose shared father resided in the group, compared to those whose father was absent. I also suggested that a common social attraction to the father may serve as a putative mechanism of kin recognition paternal half-siblings. Therefore, when a father is absent, this mechanism is less likely to operate. Perhaps social bonds among paternal half-siblings are mediated by the shared father's residence. These social bonds may, in turn, be positively associated with tolerance while feeding and which may lead to enhanced resource acquisition.

In conclusion, immatures feeding on defensible resources were more tolerant of the presence of half-siblings than nonkin and this tolerance applied to *both* maternal and paternal kin. These results also support recent studies indicating that in spite of the importance of matrilineal kinship in matrilocal societies, paternal kinship may also have important adaptive consequences

in this social context (van Schaik and Paul 1996; Palombit et al. 1997; Alberts 1999; Borries et al. 1999; Buchan et al. 2003; Charpentier et al. 2008; Nguyen et al. 2009; Huchard et al. 2012).

Future research will investigate these hypotheses by examining the impact of parents and extended kin on juvenile foraging behavior.

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CONCLUSIONS

Relationships with relatives are arguably the principal organizing feature of mammalian sociality (Blaustein et al. 1987; Hepper 1991). Studies of nonhuman primates demonstrate the important role that kinship plays in directing affiliative behaviors towards conspecifics (strepsirrhines: mouse lemurs, *Microcebus murinus*: Wimmer et al. 2002; New World monkeys: wedge-capped capuchins, *Cebus olivaceus*: O'Brien, 1993; white-faced capuchins, *Cebus capucinus*: Perry 1996, et al. 2008; howler monkeys, *Alouatta seniculus*: Pope 1990, 2000; Old World monkeys: Hanuman langur, *Presbytis entellus*: Borries et al., 1991; macaques, *Macaca* spp.: Chapais 1983; Bernstein and Ehardt 1986; Kuester et al. 1994; baboons, *Papio* spp.: Hausfater et al. 1982; Cheney 1978; Altman 1980). This nepotism is usually attributed to kin selection (Gouzoules and Gouzoules 1987; Bernstein 1991; Silk 2009).

Almost all of this research on kinship in nonhuman primates has focused on maternal relatives in female philopatric societies. One consequence of this emphasis on maternal relatives is that the adaptive significance of paternal kinship remains unclear and even somewhat contradictory. For example, unlike coalitional behaviors observed among maternal kin (Silk et al. 2004), there is variable evidence suggesting Old World monkeys support paternal kin (Widdig et al. 2001, 2002; Buchan et al. 2003). In addition, some studies demonstrate paternal half-siblings maintain stronger social bonds (Smith et al. 2003) while others report weaker bonds (Widdig et al. 2001, 2002; Silk et al. 2006). Furthermore, the empirical record is incomplete because the full range of social behaviors exhibited between paternal kin is still not known. Therefore, further exploration of these relationships and their fitness outcomes is needed before we are able fully understand the evolution of social behavior (Silk 2002).

My study seeks to contribute to our understanding of kinship by examining the social and foraging behavior of young olive baboons in association with different types of relatives. This work builds on previous studies (reviewed by Widdig 2007) and explores hypotheses generated

by kin selection. (Hamilton 1964). The data presented here shed light on the proximate and ultimate functions of paternal kinship in a matrilocal society (see Table 1).

I report that paternal half-siblings maintain social bonds of intermediate strength, between unrelated individuals and maternal half-siblings. These findings suggest that social integration may be achieved through both paternal and maternal relatives in a matrilocal society. Social integration, for adult female cercopithecines is achieved through long-term social bonds with other females (Silk et al. 2006) and is positively correlated with lifetime reproductive success (Silk et al. 2003, 2009) and longevity (Silk et al. 2010). Perhaps bonds with paternal siblings, in addition to those with maternal siblings, increase a juveniles overall integration in a social group. This study supports Charpentier et al. (2012)'s findings that in mandrills, females who received the least amount affiliation gave birth a year later than those who exhibited higher rates of affiliation. Because age of first birth is a proxy for lifetime reproductive success (Altmann et al. 1988), social integration among juveniles may significantly benefit an individual's fitness and extending sociality to paternal kin may enhance this phenomenon.

I also provide evidence that fathers mediate social bonds among their young offspring. The presence of the father was positively associated with the strength of social bonds among his offspring. This result has implications for interpreting previous studies on paternal kin. Specifically, there are discrepancies between studies reporting that affiliation among paternal half-siblings as being higher than among unrelated individuals (Widdig et al. 2001, 2002; Widdig 2002; Smith et al. 2003; Silk et al. 2006; Charpentier et al 2007), as indistinguishable from non-kin (Erhardt et al. 1997), or as being equal to those among maternal half-siblings (Smith et al. 2003). I suggest here that these discrepancies may be due to the residence of the father. Although the majority of these studies focused on adult female cercopithecines, it is possible individuals require the father to be resident during development to identify, and consequently affiliate with, paternal half-siblings.

This result may also suggest a mechanism for kin recognition. Although I did not intend to explore such a mechanism, these results offer the intriguing possibility that familiarity through associating with the father drives the recognition of paternal half-siblings. Age similarity has been offered as a possible proxy used to identify paternal kin (Altman 1979; Alberts 1999; Widdig et al. 2001; Smith et al. 2003). This assertion rests on the fact that individuals conceived during the same reproductive season are likely to be paternal half-siblings due to the correlation between male rank and reproductive success (Altmann 1979; Altmann et al. 1996; de Ruiter and Geffen 1998; Widdig et al. 2004). This mechanism, however, is not consistently demonstrated across studies examining paternal kinship and was not found here.

If familiarity with the mother mediates relationships among maternal kin (Chapais 2001), familiarity with fathers may promote relationships among paternal kin. One possibility is that youngsters may be able to identify fathers through “friendships”, which are defined by extended associations between an adult male and a lactating female (Smuts 1985). New research shows that friendships may represent a paternal care strategy (van Schaik and Kappeler 1997; Palombit 2000; Moscovice et al. 2010; Cheney et al. 2015). This inference supports other studies that suggest a broader range of individuals, besides those of the same age cohort, are able to recognize paternal kin. For example, male savannah baboons were shown to intervene in agonistic disputes on behalf of their offspring more frequently than with nonrelated juveniles (Buchan et al. 2003). Moreover, in accordance with Widdig et al. (2001, 2002), Charpentier et al. (2012) found juvenile mandrills were shown to behave preferentially with older maternal and paternal relatives compared to nonkin. In sum, if males use these postnatal relationships with females as a way to provide parental care, then offspring may be able to recognize one another through a shared association with their mother’s friend who is the putative father.

This study also found that *both* mothers and fathers were associated with enhanced foraging success among juveniles. Juveniles were able to spend a longer amount of time feeding on defendable resources when near their mothers, which suggests that the costs of contest

competition may be alleviated. This result contributes to our understanding of co-feeding between maternal kin (McGrew 1975; Silk 1979; Imakawa 1988; Belisle and Chapais 2001; Johnson and Bock 2004; Silk et al. 2004; Ueno 2005; Clarke 2010).

In addition to reaping benefits from decreased chances of harassment, youngsters may be learning various social behaviors by foraging in close proximity to adults (Pereira and Fairbanks 1993). Experience through direct observation may improve juvenile foraging skills (Goodall 1986; Boinski and Frigaszy 1989; Lonsdorf et al. 2004; Rapaport and Brown 2008; Ottoni and Izar 2008; Lonsdorf and Ross 2012). Extended feeding bouts can therefore reflect increased foraging efficiency as well as opportunities for observational learning. Although this study did not examine specifically this benefit, the results suggest this possibility.

These findings also demonstrate such social learning may be sex-specific among youngsters and their parents. Previous research has shown that juvenile primates prefer interactions with same-sex partners (Ehardt and Bernstein, 1987; Cords et al. 2010; Charpentier et al. 2012; Lonsdorf et al. 2005, 2014), which may be an attempt to maximize their ability to learn sex specific social and foraging behaviors. In this study, however, juveniles may be seeking to learn foraging and social behaviors from those same sex adults that are the most likely to tolerant their presence: their parents.

By showing that fathers can positively influence offspring foraging behavior, this study builds on previous research demonstrating the adaptive benefits of fathers (Charpentier et al. 2008; Huchard et al. 2013). These results also suggest mechanisms by which offspring may ultimately increase their lifetime reproductive success (*sensu* Charpentier et al. 2008). Fathers may be more tolerant of their own offspring than they are of unrelated juveniles and this may facilitate social learning of crucial foraging behaviors. These relationships may prove crucial for survival and reproductive success in complex and competitive groups of primates.

Finally, immatures were more tolerant of half-siblings when they were feeding on discrete, defensible resources. These results add to previous research reporting that among adult

nonhuman primates, young maternal half-siblings experienced significantly longer feeding bouts and slower feeding rates when in proximity to one another than when near unrelated immatures (McGrew 1975; Silk 1979; Feistner and Price 1990; Perry and Rose 1994; Belisle and Chapais 2001; Silk et al. 2004). This study also contributes to a body of work demonstrating that relationships among siblings are associated with presumed correlates of fitness in haplorhines (see review by Silk 2012), while highlighting the importance of *both* maternal and paternal half-siblings when foraging.

In addition to these findings, a post-hoc analysis also suggests the significance of the residency of mothers and fathers on the foraging behaviors of offspring. These results build on previously described behaviors where the presence of the father mediates relationships among paternal half-siblings (Chapter 1). These social bonds may translate into foraging success through higher rates of tolerance while feeding. Therefore, contributing to previous works suggesting fathers enhance foraging of offspring (Charpentier et al. 2008; Huchard et al. 2013), paternal half-siblings may also promote an individual's fitness.

Interestingly, juveniles without mothers in the social group spent more time foraging near maternal half-siblings than those with resident mothers. This result was in apparent contrast to findings that social bonds were unaffected by the presence or absence of the mother in the social group. While this result seems to confirm that maternal kin are important foraging partners, it does not indicate that the strengths of social bonds are likewise affected. Perhaps when a mother is no longer in the group, her offspring may spend more time co-feeding in an attempt to compensate for the loss of their main foraging partner.

Future studies will expand on these findings by evaluating the relationship between fathers and young offspring. I have argued that juveniles may be able to identify paternal half-siblings through a shared association with the father. Evaluating interactions between youngsters and adult males (e.g. by comparing fathers to unrelated adult males) will help to test the hypothesis that familiarity with a shared father drives bonds between paternal half-siblings. In

addition, exploring the role of friendships (Smuts 1985) on juvenile-father identification and social bonds will also add our understanding paternal bonds. Furthermore, examining the development of the relationships with paternal half-siblings across time and measuring fitness outcomes will help to reveal the evolutionary importance of these bonds. Such research will help to illuminate a form of kinship that we have only recently begun to understand.

I also plan to extend my analysis of the compensatory hypothesis proposed by Silk et al. (2006). Although, the results presented here do not support the predictions made by Silk et al. (2006), where individuals compensate for the loss of a mother by strengthening bonds with maternal and paternal half-siblings, this discrepancy may be due to the age of the focal individuals I used in this study. Because youngsters rely on their mothers not only as older and more useful social allies, but also for learning requisite social and foraging behaviors within their environment (Lonsdorf and Ross 2012). Juveniles who have lost a mother may be seeking to strengthen bonds with other adult relatives to further facilitate this type of learning and social development. Future analyses will explore social bonds among youngsters and adult maternal kin (such as maternal aunts) to help tease apart the flexibility of bonds among relatives.

Explanations of kin selection in nonhuman primates, and mammals more generally, have concentrated almost entirely upon matrilineal relatives in matrilineal societies. This focus overlooks a simple fact, however: individuals can be related paternally too. We are now able to take advantage of advances in genetic methods to broaden our understanding of kinship. As Silk (2002:849) emphasized in a recent review, “to fully assess the role of kin selection in primate groups, we need more...accurate information about paternal kin relationships.” Indeed, “the kinship concept” has effectively been a “black box” in part because half of the information has been missing (i.e. patrilineal kinship) (Chapais and Berman 2004: 6). Genetic techniques provide researchers with the opportunity to fully test kin selection theory and the ability to explore the adaptive significance of the paternal contribution to genetic relatedness. This study begins to rectify some of these important issues by investigating the impact that paternal kinship can have

in a matrilocal primate society which, in turn, will expand our understanding of the evolution of social behavior.

Table 4.1. A summary of all predictions made throughout the dissertation.

Chapter	Prediction	Supported?
Availability of parents determines social bonds between maternal and paternal half-sibling juvenile olive baboons (<i>Papio hamadryas anubis</i>)	Social bond strength should differ between dyad categories (i.e., maternal half-siblings, paternal half-siblings, and unrelated dyads)	YES
Availability of parents determines social bonds between maternal and paternal half-sibling juvenile olive baboons (<i>Papio hamadryas anubis</i>)	Juveniles with mothers in the group will: (a) maintain stronger social bonds with maternal half-siblings than with paternal half-siblings, (b) maintain more strong social bonds with maternal half-siblings than with paternal half-siblings	NO
Availability of parents determines social bonds between maternal and paternal half-sibling juvenile olive baboons (<i>Papio hamadryas anubis</i>)	Juveniles lacking a mother will: (a) maintain stronger social bonds with paternal half-siblings compared to those with mothers; (b) maintain an equal number of strong social bonds with both paternal and maternal half-siblings	NO
Availability of parents determines social bonds between maternal and paternal half-sibling juvenile olive baboons (<i>Papio hamadryas anubis</i>)	Compared to juveniles without fathers in the group, youngsters with fathers will: (a) maintain stronger ties with paternal half-siblings; (b) maintain more strong social bonds with paternal half-siblings; (c) maintain fewer strong bonds with maternal half-siblings; and (d) maintain weaker bonds with maternal half-siblings	YES
Mothers and fathers play a role in the development of foraging behaviors in juvenile olive baboons (<i>Papio hamadryas anubis</i>)	For foods engendering contest competition, feeding bout duration will be: (a) longer when youngsters are feeding near mothers compared to when feeding alone or near other adult females; and (b) longer when youngsters are feeding near fathers compared to when feeding alone or near other unrelated adult males	(a): YES (b): NO

Table 4.1 Continued.

Chapter Title	Prediction	Supported?
Mothers and fathers play a role in the development of foraging behaviors in juvenile olive baboons (<i>Papio hamadryas anubis</i>)	For foods requiring extractive skill (USOs), (a) feeding bouts will be longer when youngsters are feeding near same-sex parents, compared to when feeding alone, (b) youngsters will exhibit slower feeding rates when near same-sex parents compared to when feeding alone or near unrelated adults	YES
Mothers and fathers play a role in the development of foraging behaviors in juvenile olive baboons (<i>Papio hamadryas anubis</i>)	Foods that are more evenly distributed, and therefore engendering scramble competition, will not be associated with any changes in feeding bouts or feeding rates when near adults compared to when alone.	YES
Paternal half-siblings provide short-term feeding benefits	Young baboons will experience longer feeding bouts and slower feeding rates when in proximity to their (a) maternal siblings, or (b) their paternal siblings compared to feeding near unrelated individuals or when feeding alone.	YES
Paternal half-siblings provide short-term feeding benefits	Maternal half-siblings with mothers present in the group will experience feeding bouts similar to maternal half-siblings without mothers present in the group.	NO
Paternal half-siblings provide short-term feeding benefits	Paternal half-siblings with fathers present in the group will experience longer feeding bouts than those without fathers in the group.	YES

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