MALE JAPANESE MACAQUE (*MACACA FUSCATA*) SOCIALITY: BEHAVIORAL STRATEGIES AND WELFARE SCIENCE APPLICATIONS

by

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DISSERTATION ABSTRACT

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Evolutionarily, individuals should pursue social strategies which confer advantages such as coalitionary support, mating opportunities, or access to limited resources. How an individual forms and maintains social bonds may be influenced by a large number of factors including sex, age, dominance rank, group structure, group demographics, relatedness, or seasonality. Individuals may employ differential social strategies both in terms of the type and quantity of interactions they engage in as well as their chosen social partners. The objective of this dissertation is to examine sociality in adult male Japanese macaques (*Macaca fuscata*) and the varying strategies that individuals may employ depending on their relative position within a social group.

The first study examines dominance from multiple contextual measures and compares rank against social network centrality. Results from this study indicate that approaches based exclusively in aggressive interactions may not capture nuances of rank relationships and also that rank does not necessarily predict network centrality. The second study compared individual dominance rank and reproductive success based on their aggressive and affiliative behavioral strategies. Results from this study suggest that while increased aggression may enable individuals to attain high rank, males with lower rates of aggression achieve higher reproductive success. An individual’s aggressive strategy did not predict their affiliative strategy. We also see evidence for the operation of alternative mating strategies within this population. The third study used a biological markets approach to examine the relationship between male demography, social trends (directionality and chosen partner), and social centrality. Results from this study show that older individuals of higher rank are able to maintain fewer high-value social bonds as demonstrated by decreases in directed affiliation and negative correlations between rank and measures of network centrality. Conversely, younger lower-ranking males exhibit higher rates of directed affiliation and more network centrality likely as a means of maintaining multiple lower-value social bonds.

This dissertation includes co-authored material currently in review for publication with peer-reviewed journals.

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To Devin Lea

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CHAPTER I

INTRODUCTION

THEORETICAL BACKGROUND

> *"Most primate social interactions are affiliative. If an individual's survival is enhanced by the collective advantages of living in a cohesive, socially integrated behavioral unit, then an understanding of an individual's abilities to maintain affiliative and coordinated behaviors and to minimize agonistic interactions is likely to provide critical insights into the evolution of sociality and group-living in primates."*
>
> Sussman et al., 2005, Importance of Cooperation and Affiliation in the Evolution of Primate Sociality.

I.I Fundamental Importance of Dominance: Rank and Relationships

Dominance is broadly conceptualized, biologically, as the system by which individuals gain increased access to resources. The expression of dominance can vary broadly from simple to complex mechanisms. Displays of dominance are most often thought to be based on overt agonistic interactions, particularly in non-human primates. However, a number of metrics including grooming directionality, priority-of-access, or displacement behaviors can be used to draw conclusions as to the dominance/subordinance relationships between individuals or groups of individuals. Dominance relationships and structures can extend beyond two individuals and to broader social interactions such as between multiple social groups or multiple genetic lineages (Hinde, 1976).

Dominance in males is classically thought of as selecting for fighting ability and related traits such as physical size and strength as a means of gaining differential access to resources, particularly reproductive resources such as fertile females (Alberts, Watts, & Altmann, 2003; Watts, 2010; and references therein). In this way, male fighting ability becomes a means of establishing hierarchical rank. Models of dominance based on fighting ability often show an inverse-U shaped relationship between age and rank, with male condition decreasing as individuals move from prime adulthood into agedness (Watts, 2010).

However, not all studies have agreed that dominance selects for fighting ability. In the case of non-human primates, Irwin Bernstein suggested that male dominance selects for social skills over strict fighting ability (Bernstein, 1976). Bernstein described the alpha male as fulfilling "the control animal role" as the individual responsible for buffering the social group against disruption or disturbance from any number of sources. This emphasizes the importance of the protective function over the acquisition and monopolization of resources. In Bernstein's argument, an alpha male is vigorous in the defense of the group and especially infants from predators or extra-group conspecifics. Increased genetic fitness in alpha males is selecting for the social skills necessary to maintain a society (Bernstein, 1976). Thus, a true conceptual understanding of the operation of dominance must look beyond the strictly agonistic aspects of attaining and maintaining dominance rank (Bernstein, 1981). Broadly, "a well-recognized hierarchy promotes social bonds and reduces violence" (De Waal, 1986). This reduction of violence, particularly in dyadic dominance relationships and stricter linear hierarchies, can help reduce the costs of aggression (particularly the risk of injury) (Watts, 2010).

The existence or reliability of a statistical correlation between male rank and reproduction has been debated in the relevant literature. Many sources agree that there is at least some degree of correlation (Alberts et al., 2003; Bulger, 1993; Cowlishaw, 1991; de Ruiter, 1993; Majolo et al., 2012; Sukmak et al., 2014; Watts, 2010). In groups with complex multi-male systems of dominance, access to reproductive opportunities often follows the priority-of-access model: when there are multiple females simultaneously fertile and males cannot monopolize access to multiple females simultaneously, male access to these fertile females follows the established dominance hierarchy (Altmann, 1962). While rank is a primary determinant of mating success, it can be confounded by other social factors such as the extent to which coalitions are expressed within a social group (Alberts et al., 2003; Bulger, 1993), the degree of queue-jumping which occurs when a lower-ranking male successfully challenges a higher-ranking male for a mate-guarding opportunity but does not permanently alter his social rank (Alberts et al., 2003), group size such that as number of members increases the ability of high-ranking males to monopolize fertile females decreases (Cowlishaw, 1991), and energetic constraints and female choice (Alberts et al., 2003).

Separate from these confounding factors, some literature argues that rank has no correlation to reproductive access or success. In particular, Bercovitch (1986, 1992) and McMillan (1989) argued against there being a correlation between male rank and reproductive success. The Bercovitch-McMillan Hypothesis was originally built on Bercovitch’s (1986) assertion that positive correlations between dominance and reproductive activity in male savanna baboons were due in part to inclusion of subadult males in statistical analyses, and thus an inaccurate measurement of the true underlying relationship. McMillan (1989) expanded this theory onto other non-human primates, particularly rhesus macaques. Bercovitch’s primary argument against the inclusion of subadult males in analyses was that this inclusion leads to frequent type I statistical errors (Bercovitch, 1986). Cowlishaw and Dunbar (1991) challenged the validity of the

Bercovitch-McMillan Hypothesis (Bercovitch, 1986; McMillan, 1989). In response to Cowlishaw and Dunbar (1991), Bercovitch concluded that in most species of primates, dominance and reproductive success are not significantly correlated for adult males (Bercovitch, 1992). This view was supported by other earlier sources as well, as reviewed by Alberts and colleagues (2003) and Cowlishaw and Dunbar (1991). However, more studies have found support for the relationship between dominance and reproductive success than against it.

While the function and fitness benefits of dominance shows some degree of consistency, the mechanisms and structure of dominance can vary drastically between species and populations as demonstrated in a number of studies (Chaffin, 1995; Cooper & Bernstein, 2008; Flack & de Waal, 2004; Hinde, 1976). Dominance style has been widely divided into four categories – despotic, tolerant, relaxed, and egalitarian (Flack & de Waal, 2004).

Within any given dominance structure (and accompanying population), strategies for attaining and maintaining dominance may vary depending on an individual’s rival and traits such as sex, age, and physical condition (Kappeler, 2000). A study on Barbary macaques (*Macaca Sylvanus*) found that males had three interdependent competitive strategies (Kuester et al., 1998). Another study of savannah baboons found that dominant individuals engaged in randomly timed attacks against randomly selected subordinates (Silk, 2002b). This strategy appeared both effective and efficient with resulting long-term low-level stress for subordinates and minimized risk of escalated aggression for dominants.

Other studies have found similar variations between species with the same dominance structure classifications. For example, a study of Japanese, rhesus and stumptail macaques found that although all three species displayed formalized dominance hierarchies – the specifics of their dyadic interactions varied in terms of rates of approaches, aggression, and reconciliation (Chaffin, 1995). A similar comparative study was done with Assamese (*Macaca assamensis*) and rhesus macaques and their major and minor variations in dominance style (Cooper & Bernstein, 2008). The variation both within and between species illustrates the inherent importance of considering multiple influencing factors.

Two key determinants of the form and mechanism of dominance are the number of males competing for access to a resource and the abundance of that resource. A variety of behavioral and ecological factors may influence the number of males in a given social group. A study by van Schaik and Horstermann (1994) found that predation risk may increase the number of adult males in a group (Kappeler, 2000; and references therein). Other influencing factors included the number of females in a group (and thus the feasibility of male monopolization of fertile females), the temporal overlap of female sexual receptivity, the impact of these demographic influences on male reproductive strategies, and the presence or absence of infanticidal behavior (Ibid).

For example, a study on the number of males in guenon groups (genera including *Cercopithecus, Miopithecus, Erythrocebus,* and *Allenopithecus*) found evidence for variation within a single group, across groups, and among populations (Cords, 2000). Most of this variation was concluded as relating to male mating opportunities such that groups had more males when there were more estrous females. While other social and ecological factors may also have been at work, they are difficult to evaluate. Cords found both uni- and multi-male groups, which suggests that within a species some groups would necessarily have some form of male dominance structure at work while others were dominated by a single breeding male. The number and condition of the competing males must thus influence the operation of dominance.

Both scramble and contest competition, operating either exclusively or in tandem, can also have impacts on the expression of various dominance structures (Clutton-Brock & Janson, 2012; Janson, 2000). For example, females in some lemur species have the ability to override male mate competition (Kappeler, 2000; and references therein). In some lemur species, males practice alternative strategies to avoid contest competition, thus impacting group and individual expression of dominance structure and behaviors. Each one is adaptive and independently impacts female reproductive potential and thus has impacts on male mate access behaviors (Ibid). It can be assumed that scramble and contest competition also influences the expression of these behaviors in other primate systems.

Kuester and colleagues (1998) wrote “it is clear that within and between societies there is variation in dominance style”(Kuester et al., 1998). This variation can be seen both in contrasting examinations of female *versus* male hierarchical strategies and construction, as well as between populations of the same species. Additionally, other studies have described variation in the dominance gradient between populations (Patzelt et al., 2011; Thierry, 2000).

Studies on male dominance tenure in Japanese macaques found that rank and dominance tenure varied between groups. For example, a study found that males between

15-19 years of age monopolized the highest ranks while older males tended to have their rank decline with age (Takahashi, 2002). The departure of high-ranking males was often the social mechanism for changes in social rank within the study group. However, another study on Japanese macaques concluded that male rank increased with age without the decline found by Takahashi (2002) (Johnson, 1982). The reported discrepancy between these populations could be due to their environment, as Takahashi's study group was a wild population on Kinkazan Island, Japan and Johnson's population was a semi free-range group at the Oregon National Primate Research Center. This, as well as any number of other combinations of ecological and environmental factors, would appear to point towards variability in the operation of dominance structures between populations.

It is important to note that which species are examined will drive considerations and hypotheses generated. For example, many studies focusing on more despotic or linear hierarchy models have used macaques or baboons as focal populations. As reviewed by Thierry, macaques are an excellent model for the study of society due to both the similarity in kinship and demographic structures across the macaque species as well as the variation in conflict and conflict management patterns between species (Thierry, 2000). However, if one wanted to examine cooperative dominance, it might be better to use callitrichids as model species due to their proclivity for shared male reproductive access to a single fertile female.

I.II Using a Biological Market Theory Framework

"Biological markets" is a term for interactions between individuals, specifically those in which an outside observer can identify different classes of "traders" (Noë &

Hammerstein, 1994). These traders exchange commodities such as food resources, mating opportunities, or services like protection or warning calls (Ibid). Mating systems, according to this model, can be seen as a form of biological market. It is assumed that this relationship is dependent upon supply and demand. The formal properties of a biological market, as considered by Noe and colleagues are: 1) that commodities are exchanged between individuals with individuals exerting different degrees of control over these commodities, 2) that there are a number of potential trading partners to choose from, 3) that there is competition among individuals to be the most appealing trading partner with this competition taking the form of "outbidding", 4) that supply and demand determine the value of the exchanged commodities and 5) that commodities can be advertised (either honestly or falsely) (Noë, 1992, 2017; Noë & Hammerstein, 1994). These commodities can be seen as currencies used as barter and exchange between individuals.

The importance of the biological market and the form of currencies is necessary for an examination of the evolution of coalitionary behavior and alliance formation. For example, studies of baboons have illustrated the use of grooming as a major currency (Barrett & Henzi, 2006). Grooming has been observed to be traded for a number of commodities including reciprocal grooming, access to infants, mating access and (most importantly in this context) support in agonistic conflicts (Ibid). Grooming can thus be used to compensate for what may otherwise appear to be an unbalanced trade or altruistic support.

A number of hypotheses have been put forward to explain the evolution of coalitionary behavior. One of the most frequently discussed is reciprocal altruism.

Altruism is broadly defined as a behavior that “benefits another organism, not closely related, while being apparently detrimental to the organism performing the behavior” (Bercovitch, 1988; and references therein). There are three conditions necessary for altruism to emerge – lengthy lifespan, low dispersal rate, and frequent interactions (Ibid). Reciprocal altruism depends on individuals interacting frequently and repeatedly and thus developing the ability to recognize individuals. This recognition, and as a consequence the ability to know who owes what in a reciprocal model, ties back to the biological market model. As summarized by Chapais (1995), reciprocal altruism can account for alliances in two contexts: the exchange of support for support and the exchange of affiliation for support. While the supporter derives no immediately benefits, they are later repaid through support or a different currency. This also brings in the tit-for-tat model which functions to regulate reciprocal altruism. While originally used as an effective game strategy in the prisoner’s dilemma (Key & Aiello, 2000), it can also be applied to understandings of coalitionary support (Sapolsky, 2017). The premise of tit-for-tat assumes that both partners cooperate in the first “round” or interaction but in following rounds an individual does whatever their partner did in the previous round (Sapolsky, 2017). Thus, acts of altruism should be repeatedly reciprocated in a social relationship. However, if one partner fails to support the other, then it is expected that this lack of support will be repaid. This seems to function as a means of identifying and punishing those who fail to reciprocate.

Primates have been shown to reciprocate both grooming and agonistic support with individuals preferentially investing in those who have groomed or supported them the most (Schino, 2007). These behaviors have been directed at both kin and non-kin, meaning that kin selection or kin-selected altruism may also be operating (Ibid). However, it is difficult to disentangle the influences of reciprocal altruism and kin selection (Ibid). Some studies have suggested that coalitions did not function as a form of reciprocal altruism, as there was no immediate benefit to the individual who did not gain access to the resource (often an estrous female) (Noë, 1992).

Another potential explanation for coalitionary behavior is cooperation. Cooperation is seen as both separate from reciprocal altruism and an overarching umbrella under which reciprocal altruism falls (Bercovitch, 1988; Noë & Hammerstein, 1994; van Hooff & van Schaik, 1992). From the perspective of cooperation as distinct from reciprocal altruism, cooperation between adult males results from each individual pursuing his own self-interest (Bercovitch, 1988). The distinction between cooperation and altruism arises due to the fact that cooperation results in both parties gaining benefits while altruism results in the reduction of the support donor's fitness and an enhancement of the fitness of the receiver (Ibid). Costs and benefits are not parceled out according to which individual was the recipient or donor of support. Additionally, studies of baboon coalitions and consortship access observed that males who solicited assistance from other males were not more likely to gain consort access than males who respond to solicitation (Ibid). The cooperation model does not appear to take into account the biological market or exchange of currencies but rather supposes independent individuals pursuing their own interests in the same direction.

It is also important to note that the formation of coalitions can function as an alternative mating strategy with varying degrees of success. However, participation in a coalition can increase reproductive access or success for one individual in the coalition.

Coalitions thus emerge as a strategy for lower-ranking males who cannot otherwise gain consort access to a fertile female.

In summary, assigning an evolutionary explanation for these behaviors is complex. Noe in particular pointed out that there was often an exchange of currency – with grooming being exchanged for agonistic support, however did not believe this necessarily constituted reciprocal altruism (Noë, 1992, 2017; Noë & Hammerstein, 1994). In a study of social bonds in male chimpanzees, it was asserted that this same social exchange was an example of mutualism rather than reciprocal altruism (Watts, 2002). Meanwhile, another study concluded that grooming and agonistic support were associated as part of a low-cost reciprocal altruism system, sometimes termed as by-product reciprocity (Schino, 2007, and references therein). In this system, individuals often directed grooming up the hierarchy, and grooming was exchanged with rank-related benefits such as agonistic support from a higher-ranking member during an agonistic interaction (Ibid). One issue in evaluating these different claims is the inconsistency in definition through which the characteristics of reciprocal altruism *versus* mutualism *versus* by-product reciprocity are often not mutually exclusive. Thus, the same behavior or set of behaviors observed across different studies has been assigned various classifications. It is from this basic framework that we can begin to examine male social relationships.

I.III The Role of Social Bonds

A social bond has been defined generally as a strong, equitable, and enduring social relationship (Ostner & Schülke, 2014a). These social relationships result from investments that individuals make while pursuing fitness-maximizing strategies (Watts, 2002). The formation and maintenance of social relationships are critical for a number of reasons. Primarily, they function to maintain social cohesion, allow individuals to navigate socially complex situations, and have consequences for individual fitness (Hinde, 1976).

Discussing male sociality presents a unique challenge in that evolutionary conditions have favored the development of affiliative female bonds much more strongly than affiliative male bonds (Keverne, 1992; Ostner & Schülke, 2014a). Males have previously been characterized as less affiliative and more aggressive than females which, when paired with their tendency towards dispersal and transiency, has served to make females the more frequent lens through which social bonds are examined (Keverne, 1992). However, male social bonds do exist.

As with most if not all animal behavior, the formation of social bonds is ultimately influenced by the evolutionary drive for individuals to attain maximum reproductive fitness. Investing in social relationships can contribute to this overarching goal from a number of directions. Forming and maintaining social relationships can have direct influence on an individual's social status which in turn affects sexual behavior, social monitoring, and access to reproductive opportunities (Keverne, 1992). The evolutionary drive to form and maintain social relationships can have direct influence on status and thus can result in differential access to resources.

Social relationships may also be, as has been mentioned, more directly reproductive in nature. Many, but not all, male-female relationships are more short term and dependent on the female's sexual cycle.

A major mechanistic question regarding social relationships is how an individual chooses which conspecifics to socially invest in. According to a general outline provided by Kummer (1978), individuals evaluate the value of a potential social partner based on three characteristics. The first is the set of overall qualities the social partner has which includes elements such as sex, age, strength, skills, and experience (Kummer, 1978). The second is the short and long-term tendencies of the social partner, and how such tendencies align with the goals of the investing individual. And lastly is the availability of the desired social partner (Ibid). It is important to note that there is significant variation in sociality between species (which can be dependent upon social system) but also between individuals within the same species or population.

The question of measuring or classifying social relationships is multifaceted. The intensity and the means with which individuals build nonreproductive relationships is often comparable to that in a reproductive bond (Kummer, 1978; and references therein). Relationships are often most successfully studied through a focus on one member of a dyad as the subject whose goals are analyzed with the second partner as the social resource (Ibid). In this sense, a three-level structure to the study of social bonds can be created. The three levels of analysis are interactions between individuals, relationships between individuals, and population social structure (Hinde, 1976; Kummer, 1978). Interactions are a means to build or prevent a certain aspect of a relationship. A relationship is an investment which benefits the interactor and can be described by the number and types of its interactions, their quality, and their temporal patterning. These factors thus provide dimension for the analysis of variation between relationships, such as the degree of reciprocity, control, or alignment of momentary goals of both individuals (Hinde, 1976; Kummer, 1978).

I.III.I Male-Male Social Bonds

There are a number of conditions or parameters that can influence the formation of male-male social bonds. According to Ostner and Schülke (2014), male social bonds evolved as long-term alliances that gained their adaptive function in within-group contest competition. The variation in the degree to which a species or population experienced within-group contest competition drove the evolution of male social bonds. Under this model, it was concluded that medium-to-low within-group contest competition promotes the formation of political coalitions which contributes to the relative rarity of social bonds among male primates (Ostner & Schülke, 2014a).

As previously mentioned, tolerance and affiliative bonding is evolutionarily expected to occur with less frequency and ease between males than between females (van Hooff & van Schaik, 1994). However, there are a number of species in which males form strong lasting social bonds characterized by high affiliation. These bonds have been reported in red colobus species (*Piliocolobus*), hamadryas baboons (*Papio hamadryas*), Guinea baboons (*Papio papio*), spider monkeys (*Brachyteles*), chimpanzees (*Pan troglodytes*), squirrel monkeys (*Saimiri*), and bonnet macaques (*Macaca radiata*) (Boinski, 1994; Patzelt et al., 2014; Silk, 1994; van Hooff & van Schaik, 1994; and references therein). Social exchange is prominent in social relationships among male chimpanzees at Ngogo who show reciprocity in grooming and support as well as interchange of grooming given and support received (and vice versa) (Watts, 2002). This illustrates the importance of reciprocity and interchange in maintaining male social bonds in a manner that is representative of mutualism over reciprocal altruism. These results were supported in another chimpanzee study in which virtually all males were observed to establish at least one enduring and equitable social bond (Mitani, 2009).

Remarkably close male bonding has also been observed in squirrel monkeys (Boinski, 1994). Males are philopatric, there is little-to-no male-male within-troop aggression, and only slight evidence for dominance hierarchy. Most bonding and accompanying affiliative interactions are observed between same-age male cohorts with secondary less intense associations between young and full adult males (Ibid). Males cooperated in sexual investigations of females, aggressive interactions with neighbor troops, and the defense of infants and subadults from predators. Boinski (1994) intriguingly observed that affiliative associations between males were most dense over a spatial scale of five meters or less while spatial association among females never exceeded random expectations.

Adult male bonnet macaques have also been observed to frequently sit together, groom one another, huddle, greet and support each other (Silk, 1994). This is related to their participation in coalitions, as males tend to support the males with whom they associate and interact affiliatively. These observations support the determinants of male bonding outlined in previous studies (Ostner & Schülke, 2014b; van Hooff & van Schaik, 1992, 1994). Another study of Guinea baboons found that males exhibit strong tolerance and bonds (Patzelt et al., 2014). Within Guinea baboons, “units” of males with their associated females form “parties” which team up as “gangs”. Males formed strong bonds within parties which were not correlated with genetic relatedness. Agonism between these males was rare. Additionally, although Guinea baboons have a social organization similar to that of hamadryas baboons, the observed male-male affiliation was stronger in Guinea baboons and included both more elaborate greeting rituals between the adult males and less aggression towards females (Patzelt et al., 2014).

Environmental or socioecological factors can be another determinant of social bonding. These factors can determine relationships between females, which in turn can determine the relationships formed between males (van Hooff & van Schaik, 1994). In essence, the type and form of resource competition can effect fundamental aspects of social organization which in turn influence the type and strength of social bonds (Ostner & Schülke, 2014a; van Hooff & van Schaik, 1994). Previous studies of captive stump-tailed macaques (*Macaca arctoides*) have classified social relationships as tolerant due to relatively high rates of affiliation, frequent aggression, and symmetrical conflicts (Richter et al., 2009). A comparative study on provisioned semi-free ranging male stump-tailed macaques found less affiliation and found that most affiliation was directed towards higher-ranking males (Ibid).

Another study of macaques found that uneven sex ratios lead to concentrated grooming between females or between females and their offspring whereas groups with even sex ratios had more males available as alternative grooming partners (Hill, 1994). As a result, male affiliative behavior was more frequently observed in smaller groups with more even sex ratios. Similarly, both provisioning and highly disparate sex ratios can result in increased within-group aggression and tension (Ibid). A third comparative study of atelines found that male dominance over females can be associated with within-group contest competition and hierarchical relationships (Strier, 1994). It was also suggested that the ability of males to dominate females is an important -determinant of whether within group competition among males is of the contest or scramble type, which in turn influences the formation of male bonds (Strier, 1994). These findings lend support to the importance of social environment and group demographics in influencing the expression of male affiliation and male social bonds.

Relatedness may also be a significant influence on the pattern of male bonding observed in certain species, but isn't necessarily a factor in all male bonds (Cheney et al., 1986; Silk et al., 2013; van Hooff & van Schaik, 1994). Studies of bonobos and chimpanzees have suggested that kinship plays an important role in male bonding. Rates of affiliative interactions between males are similar between the two species despite a differential distribution of females (Furuichi & Ihobe, 1994). Male bonding in these species could be a reflection of male philopatry and thus relatedness, but the form this bonding takes is determined by competition over females (van Hooff & van Schaik, 1994). Another study focusing solely on chimpanzees found that relationships formed based either on maternal kinship or on equality judged by balanced grooming interactions (Mitani, 2009). Kinship was judged to be an unlikely factor in male macaque relationships due to frequent movement between groups (Hill, 1994). Similarly, Strier (1994) ultimately proposed that kinship did not necessarily lead to strong affiliative relationships or cooperation among male group members in atelines.

Many of these factors have ultimately referenced the importance of the selective pressures of between group competition and within group competition on male affiliation and relationships (Ostner & Schülke, 2014a; van Hooff & van Schaik, 1992, 1994).

I.III.II Male-Female Social Bonds

Male-female social relationships can serve a number of different purposes. Some of these long-term relationships have been observed to function as an alternative mating strategy (Goffe et al., 2016; Nguyen et al., 2009; Smuts, 1985). Female primates will sometimes form special male friendships. In these friendships, the male and female will spend a large portion of time together, groom each other often, and appear relaxed in one another's company (Smuts, 1985). These friendships can continue for many months, through both pregnancy and lactation when a female is not sexually receptive. Some have been observed to last at least 6 years (Cheney et al., 1986).

As previously mentioned, paternal investment could also influence male-female relationships. Females (and their offspring) have been observed to form lasting friendships with the genetic fathers of their offspring (Nguyen et al., 2009). This type of investment has clear immediate fitness benefits for the investing male. However, investment in offspring can also be an alternative mating strategy.

Intriguingly, female baboons (*Papio cynocephalus*) and their offspring have also been observed forming these long-lasting friendships with males who were almost certainly not the genetic father of the offspring (Nguyen et al., 2009). These males had not been observed to consort with the female during the days most likely for conception, so this behavior did not appear to be explained by paternity confusion. There was no evidence that these friendships increased the male's chances of mating in future reproductive cycles. There may have been psycho-social benefits to these friendships, likely following the previously described biological market model in which the male and female were exchanging non-reproductive resources (Barrett & Henzi, 2006; Noë, 2017; Noë & Hammerstein, 1994).

Relationships may also be cyclical in nature, alternating between reproductive and non-reproductive stages. In these cases, females are expected to interact heavily with males with whom they copulate. However, these relationships persist across sexual cycles with no significant variation. This indicates a long-term relationship which necessitates maintenance beyond the directly reproductive period. This has been observed in Guinea baboons where females formed relationships with both primary and secondary males (Goffe et al., 2016). The relationships with primary males were both affiliative and reproductive in nature – but not significantly influenced by the reproductive cycle. These relationships remained stable and with little variation during the estrous phase. A smaller subset of females also formed weaker affiliative but nonsexual relationships with secondary males. While the primary male relationships have reproductive elements, the separation from the reproductive cycle would suggest a long-term social bond from which reproductive access is a benefit but not the entire basis.

An earlier study of baboons similarly described three types of long-term social bonds between adult males and adult females (Seyfarth, 1978). The first type of bond described was a persistent, high-frequency bond in which male and female dyads maintain frequent proximity and grooming regardless of the female's reproductive state. The second bond was termed a persistent, low-frequency bond in which females showed preference for the dominant male over more subordinate males across all reproductive states and attempted to establish high-frequency social bonds with the dominant male. This attempt was unsuccessful due to a persistent high-frequency bond the dominant male had already formed with another female as well as competition between females. The last bond was described as being based on “alternating” female preference in which females associated mostly with a subordinate male during lactation and with the dominant male during sexual cycling. Observations suggest that subordinate males attempted to maintain these bonds into the females’ periods of sexual cycling (Seyfarth, 1978).

The last type of male-female relationship described is kinship based, particularly those between females and their adult male offspring. These enduring mother-son relationships can be expected when 1) the female competition regime allows female emigration, which allows a male to stay with his mother and 2) sexual dimorphism is limited (van Hooff & van Schaik, 1994).

I. IV Impact of Kin Selection and Offspring Investment

Kin recognition is a critical adaptation that allows males to selectively invest in immatures, and thus a key mechanism in the operation of kin selection (Chapais, 2001; Eberhard, 1975; Silk, 2002a). The theory of kin selection, first proposed by Hamilton (1964), has become a staple theory in the evolutionary study of altruism and particularly paternal kin recognition in primate species (Ibid, and references therein). The fitness benefits of investing in offspring can be direct or indirect. A male who gains direct fitness benefits is expected to produce both a higher quality and quantity of offspring as a result of offspring investment. If such investment does not result in higher quality and quantity of offspring, investment is not selected for. This form of paternal investment appears to have been adaptive in some but not all primate species, as paternal care may have evolved independently a number of times in primates (Fernandez-Duque et al., 2009).

The paternal investment hypothesis proposes that males invest in their own progeny or other genetically related infants (Paul, Kuester, & Arnemann, 1996; and references therein). In the case of male investment in related but not direct offspring, the underlying assumption is that the cost of lost reproductive opportunities for the male in question does not outweigh the benefits of investing in the genetically related immature. Hamilton’s selection theory also outlined the paradigm by which this behavior is governed, namely that the degree of relatedness governs the benefit the investing male receives, and thus the worth of his investment (Hamilton, 1964). Studies on primates have found that individuals recognize paternal kin (Buchan et al., 2003; Murray et al., 2016). While the exact mechanisms of this recognition are difficult to determine, some have suggested that a wide variety of cues could be in use including behavioral cues, age proximity, residence patterns, and prior mating behavior (Tang-Martinez, 2001).

Kin recognition is thus necessary for both direct and indirect investment in immature genetic relatives. However, despite the potential fitness benefits of investment, there is high variability in the frequency and intensity of these behaviors in adult males across primate taxa (Kleiman, 1985). Additionally, although not an operation of kin recognition or kin selection, male investment in non-kin immatures can also be selected for via direct fitness benefits. Male investment in non-kin immatures does not require the evolution of kin recognition systems, but it also doesn’t select against the evolution of these mechanisms. And, as will be shortly discussed, there is evidence for increased breeding opportunities for those males who strategically care for unrelated immatures.

The evolutionary and strategic benefits of kin selection and wider investment in juveniles by adult male primates has thus been selected for under multiple avenues as will be discussed. However, there is great variation in this behavior not only between but within species. Furthermore, there are a number of mechanisms by which males invest in immatures.

A number of studies have reviewed the specific behaviors deemed “paternal” or characteristic of paternal or male care (Smuts & Gubernick, 1992; Van Schaik & Paul, 1996). These behavioral forms of offspring investment can be broadly divided into two categories – a subset of behaviors nurturing in nature and a second subset of behaviors protective in nature.

Nurturing type investment includes such behaviors as infant carrying, grooming, playing, sharing food, feeding, cleaning, retrieving, huddling, babysitting or teaching (Fernandez-Duque et al., 2009). These behaviors differ from the protective category in being characterized as direct, conspicuous, and sustained across a time and circumstance (Ibid). Extensive carrying by adult males (putative fathers) has been observed in a number of non-human platyrrhine genera including *Aotus, Callicebus, Saguinus, Cebuella, Leontropithecus*, and *Callithrix* (Garber & Leigh, 1997; Wright, 1990). This suite of behaviors is especially visible in titi monkeys (*Callicebus*) and owl monkeys *(Aotus*). In both species, the male is the primary carrier of the infant with dependent infants carried as much as 90% of the time by the adult male (Fernandez-Duque et al., 2009; and references therein). In some cases in titi monkeys, infants even develop a preference for their fathers over their mothers (Ibid).

This pattern of heavy direct nurturing investment is not restricted to smaller bodied primates. Siamangs (*Symphalangus syndactylus*) are the only hylobatid to display extensive paternal care, which is done in a specific manner (Fernandez-Duque et al., 2009; and references therein). The adult female takes exclusive responsibility for the infant in the first year of life, but in the second year the infant is primarily carried by the adult male and older juvenile offspring (Ibid). This type of alloparental care is not highly characteristic of hylobatids nor has it been as extensively observed in other catarrhine species as it has been in South American callitrichids (Ibid). Some have thought that this behavior may be related to the monogamous system in which the male siamang can be reasonably sure of paternity – however, this has not translated to similar behavior in other socially monogamous hylobatid species. Furthermore, social monogamy may be only a single potential influencing factor of these behaviors.

A study by Busse and Hamilton (1981) also observed infant carrying in male chacma baboons (*Papio ursinus*). Male chacma baboons were found to particularly carry their offspring during confrontations with immigrant males, presumably due to the threat these immigrant males posed to infants (Busse & Hamilton, 1981). Furthermore, infants were observed to sometimes initiate confrontation by approaching immigrant males in the presence of more protective resident adult males. The mothers of these infants were not observed interfering in this behavior. However, the conclusions of this study were based on identifying “probable” fathers but without genetic paternal certainty. There was no conclusive evidence as to whether males were able to identify their own offspring or if this carrying response was generalized to all infants (and thus potential offspring) in the social group (Ibid). This behavior, while nurturing, could also be classified as protective in function.

In terms of more strictly protective type behaviors, males have been known to lend agonistic support to immatures in varying degrees across multiple taxa. A 2016 study of Assamese macaques (*Macaca assamensis*) found that while immatures were responsible for maintaining spatial proximity to their preferred adult male, these preferred males would protect the infant against harassment or antagonism in the absence of the protective mother figure (Minge et al., 2016). This study found that preferred males supported immatures in conflicts more often than nonpreferred males and that infant proximity to the preferred male was negatively associated with the presence of the mother and positively associated with the presence of nonpreferred males (Ibid).

This protective behavior has been more concretely studied in gelada baboons (*Theropithecus gelada*). Although gelada baboons live in harem-style social communities, a deposed harem leader has often been observed to remain in the social group and actively protect the group infants (Van Schaik & Paul, 1996; and references therein). These deposed males rarely mate. This form of protection against infanticide (with relatively few or no mating benefits) has also been observed in long-tailed macaques and chacma baboons (Ibid). The observation of these behaviors raises the question of what circumstances make infant investment adaptable.

It has often been suggested that paternal investment can be positively associated with the degree of paternal certainty (Fernandez-Duque et al., 2009; Garber & Leigh, 1997). Paternity certainty has been considered a critical selective force favoring the evolution of male care in humans (Smuts & Gubernick, 1992). However, the paternity certainty hypothesis has not been an adequate explanation for the evolution of male care of young in non-human primates (Ibid). This is partially due to the fact that male care is not exclusively correlated to or predicted by parentage (Van Schaik & Paul, 1996).

Males can have high paternity certainty in monogamous species. As a result, some studies have generalized male investment in juveniles (such as high paternal care and provisioning of the young) as being characteristic or influenced by monogamy (Fernandez-Duque et al., 2009; Garber & Leigh, 1997). However, male care is not found in every monogamous species – such as the hylobatids in which only the siamang has been observed to have high paternal investment. Thus it would appear that high paternal certainty alone does not elicit a high degree of male care of infants (Van Schaik & Paul, 1996). This fact has been used to argue that extensive paternal care is not necessarily associated with monogamy or paternal certainty (Wright, 1990). This may suggest that male care is not a consequence of monogamy, but could have preceded monogamy and influenced the evolution of pair-bonding behavior (rather than vice versa) (Smuts & Gubernick, 1992).

The importance of monogamy in deciding degree of paternal care is further called into question when examining genera such as *Macaca* and *Papio*. Although not characteristic of every species, some male primates living in multi-male multi-female social groups with a polygynandrous mating system have been shown to selectively direct care towards their own genetic offspring (Langos, Kulik, Mundry, & Widdig, 2013; Buchan et al., 2003; and references therein). While this would still support paternal certainty as a selecting factor (to some degree), there are examples of males outside of monogamous systems investing in non-kin immatures with little to no paternal certainty.

Another proposed condition that influences paternal care is the degree of female energetic investment. Studies of callitrichids have argued that males serving as infant transporters is necessary to allow females to maintain high birth rates, litter weights, and litter growth rates (Garber & Leigh, 1997; Key & Aiello, 2000; Kleiman, 1985; Wright,2009; and references therein). Under this model, paternal care is best understood in terms of the relative reproductive effort of both sexes. A study by Key and Aiello (2000) found that when male reproductive cost is equal to or less than 10% of female reproductive cost, males will invest in females and their offspring despite the costs in time, energy and lost mating opportunities. This expression of non-reciprocal altruism was observed regardless of whether the male mated with the female (Key & Aiello, 2000). It was hypothesized that it may be advantageous for the male to invest in those females "likely to become mothers of their own offspring" (Key & Aiello, 2000).

These studies would appear to suggest that while paternal certainty or female investment can be predictive of paternal care, they are not exclusive or certain predictors. Furthermore, the conditions under which a species or a specific individual develops a pattern of paternal investment are presently unclear and likely the result of a complex assortment of environmental, social, and other influences.

I.IV.I Investment in Non-Kin Immatures

Although paternal care mechanistically and evolutionarily influences male investment of immature kin, there is also evidence that adult males will knowingly invest care and energy in non-kin immatures. Evolutionary models for male investment in immatures (both kin and non-kin) include the mating effort hypothesis, the agonistic buffering hypothesis, and the paternal investment hypothesis. Some of these strategies may actually favor investment in non-kin immatures over offspring. For example, one study found evidence that male-immature affiliation (but not father-offspring) could impact the fitness of immatures (Langos et al., 2015). However, an examination of each proposed hypothesis is necessary for building a fundamental understanding of the evolutionary adaptiveness of this behavior.

The mating effort hypothesis is based on a mutually advantageous and reciprocal relationship between males and females (Smuts & Gubernick, 1992). The mating effort hypothesis, as reviewed by Smuts and Gubernick (1992), predicts that male care of immatures is most likely under the following conditions: 1) infants can benefit from male care, 2) females or infants can control and offer important benefits to males, and/or 3) females (or infants) have opportunities to compare the behavior of different males and then, on the basis of this comparison, distribute benefits to some males and not to others. The benefits to males under the mating effort model is increased reproductive access to the mothers of infants or to other observing females. It is important to note that paternal behavior is better explained under the mating effort model in species or social environments in which female choice is evident and effective (Van Schaik & Paul, 1996).

This means that male care as a function of the mating effort hypotheses should be more common in multi-male systems where females can, in principal, choose between males (Van Schaik & Paul, 1996, and references therein). Vervet monkeys (*Chlorocebus pygerythrus*) have been observed to be more affiliative with infants when the infant’s mother was in visual contact (Ibid). In multi-male gelada units, the follower (non-dominant) male was observed to affiliate with the group’s infants which was hypothesized to be a means of establishing sexual relationships with the infants’ mothers (Ibid). Similarly, in cotton-top tamarins (*Saguinus oedipus*), males were found to be more attractive as mates when carrying offspring (Ibid). However, the mating effort hypothesis alone is not sufficient to address all instances of directed care of immatures by males as some observed instances have no discernable reproductive advantages.

A second proposed evolutionary model for male care is the agonistic buffering hypothesis. The agonistic buffering hypothesis proposes that males use infants or immatures as a means of regulating their social relationships and interactions with other adult males (Busse & Hamilton, 1981; Paul et al., 1996; and references therein). This hypothesis has been proposed to explain infant carrying in savannah baboons, however not all instances of this behavior can be attributed to agonistic buffering in this species (Busse & Hamilton, 1981). Support for this hypothesis has been specifically found in Barbary macaques (*Macaca Sylvanus*) (Paul et al., 1996). Barbary macaques, particularly subordinate males, have often been observed carrying infants towards other males which has been suggested to function as a social tool to stabilize and secure relationships between these subordinates and more dominant males (Paul et al., 1996; and references therein). This study of Barbary macaques found three lines of support for this hypothesis: 1) the direction of at least one type of triadic interaction (between two adult males and an infant) was significantly biased towards higher-ranking males, 2) the patterning of triadic interactions was strongly dependent of the rank distance between the males and 3) interaction frequency increased significantly during periods of high inter-male tension (Paul et al., 1996). However, the use of infants as a social means of agonistic buffering does not exclude simultaneous operation of either the mating effort hypothesis or the paternal investment hypothesis.

The paternal investment hypothesis predicts that males should 1) preferentially interact with paternally and/or maternally related infants and that 2) these male-infant relationships should increase the infant's chances of survival and future reproductive success (Boose et al., 2018; Paul et al., 1996). The paternal investment hypothesis can be seen as a variety of the kin selection hypothesis which predicts that infant handling provides positive fitness benefits for mothers, infants, and/or handlers (Boose et al., 2018; Mitani & Watts, 1997). Often under this model, biparental care is either necessary for successfully rearing offspring or significantly increases the fitness of offspring (Key & Aiello, 2000). Studies of chacma baboons have observed males forming bonds sometimes attributed to paternity (Van Schaik & Paul, 1996). Similarly, a study of infant carrying in savannah baboons attributed this behavior to paternal investment/effort rather than agonistic buffering as had been previously observed or hypothesized (Busse & Hamilton, 1981).

The potential benefits of longitudinal investment can also be seen in the previously discussed gelada example in which males who lose their dominant position remain in the group as a protective figure to their infants despite not gaining mating opportunities (Van Schaik & Paul, 1996). This has also been seen with long-tailed macaques in which ousted dominant males have been observed to remain in a social group in which they have lost mating access and social rank as a protective figure to his presumed infants until the infants are weaned (Ibid). A third study of chimpanzees found that males associated more with their own offspring than they did with non-kin infants, particularly early in the infants' life (Murray et al., 2016). These interactions between fathers and mother-infant pairs did not predict the probability of that male siring the mother's next offspring which indicates more support for the paternal investment hypothesis than the mating effort hypothesis (Ibid). Currently, no single hypothesis can be generalized as an explanation for every occurrence of male investment in juveniles.

However, there are also plenty of examples of male care of non-kin immatures which do not readily fall under the evolutionary umbrella of any of these hypotheses. For example, a helper system in which adult males provide care for infants they can't possibly have sired has been observed in some species of callitrichids both in wild and captive populations (Van Schaik & Paul, 1996). Studies of savannah baboons have found that males care for infants that they are unlikely to have sired (Smuts & Gubernick, 1992; Van Schaik & Paul, 1996; and references therein). In one study, males were observed to protect and have affiliative interactions with the infants of their female friends (Moscovice et al., 2009). These males intervened on the behalf of the offspring of their friends more often than on behalf of unconnected juveniles and did not appear to differentiate between genetic offspring and unrelated juvenile offspring of friends (Ibid).

Recent studies have also found evidence for non-paternity-based affiliation towards immatures in mountain gorillas (*Gorilla beringei beringei*) (Rosenbaum et al., 2015, 2016). Relationships between immatures and adult male gorillas were found to be based on the adult male's dominance rank rather than paternity. Although mountain gorilla morphology suggests an evolutionary history of single-male units (as is seen in other gorilla species), a number of groups under observation by the Karisoke Research Center contain multiple breeding adult males – meaning that these individuals do not have paternity certainty (Rosenbaum et al., 2015). Infants were observed to prioritize spatial proximity to high ranking males over low ranking males, and high ranking males directed less aggression at immatures than did low ranking males (Ibid). This particular study was able to genotype a large portion of the adult males and immatures, which showed that high ranking males had close relationships with immatures they did not sire (Ibid). Furthermore, these relationships have been demonstrated to persist longitudinally across both developmental classes and social upheaval (Rosenbaum et al., 2016).

Some degree of investment in non-kin immatures may be correlated to rank, age of the investing male, and/or sex of the immature (Alexander, 1970; Langos et al., 2013; Rosenbaum et al., 2015). Langos et al. (2013) concluded that investment was both a facet of infant sex and the age of the focal male, with older males investing in juveniles more than younger males and males preferentially investing in male immatures rather than females. This may be a form of early alliance formation. Rank was particularly predictive of male investment in a longitudinal study on Japanese macaques (as well as that already discussed in mountain gorillas). In the case of the Oregon troop of Japanese macaques (*Macaca fuscata*), higher ranking males formed intense affiliative attachments with juveniles during the pregnancy and birthing seasons (Alexander, 1970). Two of the immatures observed with male carers were orphans whose mothers had been dead for at least a year, meaning the males could not have been investing in future mating opportunities with their mothers. One particular female juvenile in the group was actively defended and cared for by the third-ranking adult male. When the female reached sexual maturity, she did not mate with this protective male (although both the female and the male actively mated with other partners). This third-ranking male engaged in similar behavior with a two-year old male after the death of that juvenile’s mother, a crippled female juvenile, and a juvenile female with a living but inattentive mother. In the case of this troop, both age and rank were predictive of investment in non-kin immatures.

Whether these examples of investment in non-kin can be attributed to poor mechanisms of kin recognition or not is unclear. However, there are clear multi-species examples of persistent male investment in non-kin immatures.

I.V Complexity of Social Systems and Networks

Various terminology has been used to describe how non-human primates form and maintain social units, often with the exact definition of a given term either conflicting between publications or conflating with other frequently used terms. For this dissertation, I will use the following definitions. Social system is an overarching term used to refer to the social organization, social structure, mating system, and care system observed in a given population or species (Kappeler, 2019; Kappeler & van Schaik, 2002). Social organization specifically refers to a group's size (both in terms of whether individuals are solitary, pair-living, or group-living as well as the number of individuals in a given group), composition, and kinship pattern. Often times, aspects such as spatial variation, temporal variation, sexual segregation, and adult sex ratio also fall under the purview of social organization (Kappeler, 2019; Kappeler & van Schaik, 2002). Social structure refers primarily to a framework for describing communication and social interactions including relationships, social bonding, dominance hierarchies, and between-group relations. Mating system addresses which individuals mate and which individuals reproduce including patterns of mating opportunities and reproductive skew. Mating system will also describe whether alternative mating strategies are used, the division of reproductive labor, and whether a given species or population engages in singular or plural breeding (Kappeler, 2019; Kappeler & van Schaik, 2002). Finally, care system defines which individuals in a group care for immatures including patterns of parental care, allo-parental care, cooperative breeding, helper dynamics, and caste polymorphism.

Of particular importance in this dissertation is the type of social structure – particularly the type of dominance hierarchy – observed in a given population or species. Variation in social structure has been particularly well-studied and documented within baboons and among both macaque and baboon species (Adams, Ostner, et al., 2015; Balasubramaniam et al., 2012; Flack & de Waal, 2004; Thierry, 2000). Social structures specifically relating to dominance have been studied since 1989 with the introduction of the term "dominance style" as a concept referring to species-typical patterns of expressed asymmetry in agonistic relationships (de Waal & Luttrell, 1989; Flack & de Waal, 2004). Typically, dominance styles have been classified under four terms: "despotic", "tolerant", "relaxed", and "egalitarian". The despotic dominance style, found in macaque species such as rhesus (*Macaca mulatta*), longtailed (*Macaca Silenus*) and Japanese (*Macaca fuscata*), is characterized by formalized relationships and large dyadic asymmetries which are reinforced through severe aggression (Flack & de Waal, 2004; Watts, 2010). This form of structure is the one most closely associated with hierarchy wherein access to resources is based on social power rank and conflict reinforces these rank relationships. Tolerant dominance, found in pig-tailed (*Macaca nemestrina*) and stump-tailed macaques (*Macaca arctoides*) as well as chimpanzees, also has formalized relationships however the large dyadic asymmetries are reinforced through more moderate to mild aggression (Ibid). This form of dominance structure is associated with an informal oligarchy in which resource access is less strictly determined by social power rank and there is some impartial policing or with a constrained system with leveling coalitions and policing.

Relaxed structures, potentially associated with crested macaques (*Macaca nigra*), have some dyadic asymmetries that are formalized relationships (Ibid). However, most relationships are unresolved and reinforcement of existing relationships is through aggressive displays rather than direct altercations. This structure is associated with an equal outcome system maintained by coalitions against individuals and mediation by powerful individuals. In this system, there may be equal access to resources. Lastly, the egalitarian structure has rare dyadic asymmetries and few temporally stable differences in social power (Ibid).

Dominance styles are fundamental to understanding and assessing both large group networks and within-group relationships. In species or populations which exhibit more structured hierarchies or despotic dominance styles, the relative rank of any two individuals in a dyadic interaction will significantly impact how they relate to each other and the directionality of key social behaviors. Each individual’s rank within a social group underpins their interactions both on the dyadic and group-wide level. Thus, this element of social structure is particularly important for studying social bonding, relationships, and strategies.

In assessing the dominance style of a given population, observers often rely on measures of steepness. Steepness is used as a measure of functionality such that a steeper and thus more highly linear hierarchy indicates a more despotic structure. Statistically, the measurement and discussion of linearity is complex (De Vries et al., 2006). The De Vries et al. (2006) methodology relies on a large matrix of dyadic interactions in order to establish an accurate hierarchical system, though this methodology does not always elicit a strict linear result. Thus, understanding the degree of steepness and expected linearity provides an understanding of the forms of dominance at group and individual levels in a given population.

Where a species or population falls on the continuum from despotic to tolerant is also crucial for understanding social networks. Network theory, although originating in mathematical graph theory, has been applied to a number of fields including sociology, business, markets analysis, political science, and biology (Wey et al., 2008; and references therein). A social network is a means of analyzing social relationships at a larger scale and incorporates measures of individuals (or units of individuals) and the ties between any two given individuals or units (Wey et al., 2008). Networks can be directed or undirected. In directed networks, there is the potential for imbalance or inequality in a relationship between two individuals or units which is often calculated based on initiation and reception of certain social behaviors (Makagon et al., 2012; McCowan & Beisner, 2017; Wey et al., 2008). Of particular utility within the study of animal behavior and welfare is the ability to examine the importance of a particular individual (or unit) to the overall social population. Studies have examined, among many other things, the impact of removing key individuals from a social network and resulting impacts on group stability (Beisner et al., 2011), seasonal variation in networks and strength of relationships (Brent et al., 2013), and immigration success (Kawazoe & Sosa, 2019). Social networks thus represent a significant tool in both the study of wild populations and in captive management of social populations.

I.VI Genus *Macaca*

The genus *Macaca* (commonly called macaques) belongs to the cercopithecid Tribe Papionini along with the genera *Papio, Theropitehcus, Lophocebus, Rungwecebus, Cercocebus,* and *Mandrillus.* The exact number of macaque species is debated - while the International Union for Conservation of Nature (IUCN) currently recognizes 22 species (not including subspecies), a generally accepted 23rd species (*M. leucogenys*) was discovered in 2015 (Table 1.1) (Flack & de Waal, 2004; Fooden, 1980; IUCN, 2020; Li et al., 2015). Extant species of macaques have traditionally been divided into four subgroups based on distinctive morphology of the glans penis: the *silenus-sylvanus* group, the *sinica* group, the *fascicularis* group, and the *arctoides* group (Fooden, 1976). Fooden (1976) did not include some species not yet identified at the time or previously classified as subspecies including *M. leonina, M. munzala, M. pagensis, M. siberu,* and *M. leucogenys*. These same species were also not included in the assessment of dominance style across macaque species previously cited (Flack & de Waal, 2004).

The various species of macaque have a considerable geographic range spanning a range of habitats including tropical and temperate ecosystems, evergreen primary forests, grasslands, mangrove swamps, semi-deserts, mountains, deciduous forest, woodlands, and human-occupied territories (Thierry et al., 2004). Macaques have the widest geographic range of all non-human primate genus. They range extensively through South and East Asia and have a single species (*M. sylvanus*) ranging as far as North Africa (Fooden, 1976, 1980). In addition to being the only remaining African representative of the genus, *M. sylvanus* is generally thought to be the most ancient *Macaca* species (Thierry et al., 2004).

There is significant variation in adult body weight and reproductive maturity, both of which are also heavily dependent on the quality and quantity of food intake as well as species-specific variations (Thierry, 2011). In terms of reproduction, females generally reach sexual maturity between 2 to 5 years of age, give birth to their first offspring between 4 and 6 years of age, and remain fertile until 20-25 years of age. Male maturation is similarly linked to food quality and availability. Generally, males begin to sexually mature between 3 and 4 years of age with testicular enlargement and continue increasing in weight, testosterone, and rates of agonistic interactions with other males over the following two years (Thierry, 2011). While males may be fully sexually mature by age 4 or 5, many do not actually begin reproducing until 7 to 11 years of age when they have reached full body size and are able to compete with other males for dominance rank and resulting access to fertile females (Ibid).

As was reviewed in section I.V (The Complexity of Social Systems and Networks), species of *Macaca* exhibit significant variation in various elements of the social system, including dominance style (Table 1.1). However, some social characteristics, particularly in terms of social organization, are consistent. Macaques typically form multi-male multi-female social groups with female philopatry and male dispersal (Balasubramaniam et al., 2018). As a result of female philopatry, macaque social groups typically have a female-biased adult sex ratio (Thierry et al., 2004). Furthermore, females are known to form kin-bonded subgroups or hierarchies (particularly in species with more despotic dominance styles) which are absent in males due to their transfer between groups upon maturation. Neighboring groups may have overlapping home ranges (Thierry et al., 2004). Although there is significant variation between *Macaca* species in social structure and dominance style, hierarchically-organized species all form both male and female hierarchies. There is also consistency in mating system with all macaque species exhibiting polygynandry.

Table 1.1: Overview of the *Macaca* Species, Statuses, and Dominance Styles

Scientific Name	**Common Name**	**IUCN Status**	**Dominance Style** [a]
M. arctoides	Stump-tailed Macaque	Vulnerable	Grade 3
M. assamensis	Assam Macaque	Near-Threatened	Grade 3
M. cyclopis	Formosan Rock Macaque	Least Concern	Grade 1
M. fascicularis	Crab-eating Macaque	Vulnerable	Grade 2
M. fuscata	Japanese Macaque	Least Concern	Grade 1
M. hecki	Heck's Macaque	Vulnerable	Grade 4
M. leonina	Northern Pig-tailed Macaque	Vulnerable	-
M. leucogenys	White-cheeked Macaque	*Status Unknown*	-
M. maura	Moor Macaque	Endangered	Grade 4
M. mulatta	Rhesus Macaque	Least Concern	Grade 1
M. munzala	Arunachal Macaque	Endangered	-
M. nemestrina	Southern Pig-tailed Macaque	Endangered	Grade 2
M. nigra	Crested Macaque	Critically Endangered	Grade 4
M. nigrescens	Gorontalo Macaque	Vulnerable	Grade 4
M. ochreata	Booted Macaque	Vulnerable	Grade 4
M. pagensis	Pagai Island Macaque	Critically Endangered	-
M. radiata	Bonnet Macaque	Vulnerable	Grade 3
M. siberu	Siberut Macaque	Endangered	Grade 4
M. Silenus	Lion-tailed Macaque	Endangered	Grade 3
M. sinica	Toque Macaque	Endangered	Grade 3
M. sylvanus	Barbary Macaque	Endangered	Grade 3
M. thibetana	Tibetan Macaque	Near-Threatened	Grade 3
M. tonkeana	Tonkean Macaque	Vulnerable	Grade 4

[a](Flack & de Waal, 2004)

Macaca has been considered one of the most successful primate genera and has emerged as a pivotal taxonomic group within primatological and biomedical research. As of 2004, macaques are the most common non-human primate genus in laboratory studies and rhesus macaques (*M. mulatta*), in particular, are the most common species (Carlsson et al., 2004; Hannibal et al., 2017). In a global overview of primates in laboratory research, rhesus macaques represented 18.4% of research subjects in scientific journal articles published in 2001 and crab-eating macaques (*M. fascicularis*) followed at 8.6% (Carlsson et al., 2004). Also featured in peer-reviewed journal articles in descending order of frequency were *M. nemestrina*, *M. fuscata*, *M. radiata*, and "Other or unspecified *Macaca*" (Carlsson et al., 2004). This prominence in laboratory research paired with extensive global study of various species *in situ* has resulted in the macaque genus being one of the most recognizable and frequently studied groups of non-human primates globally. However, the thoroughness and extensiveness of study varies depending on the particular species.

I. VII Japanese Macaques (*Macaca fuscata)*

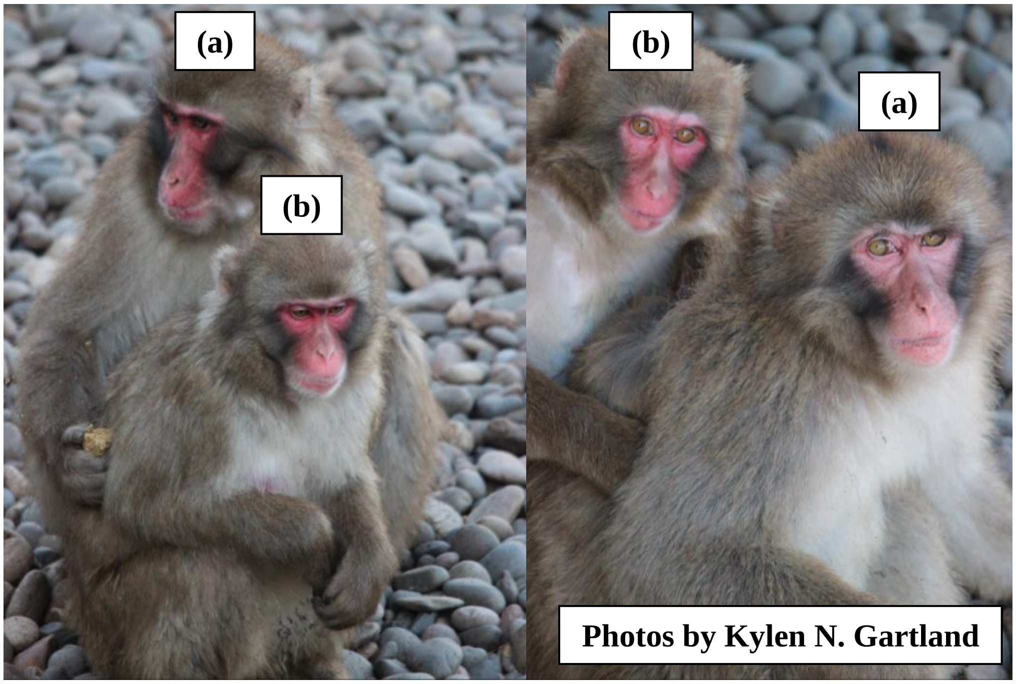
Macaca fuscata is commonly known as the Japanese macaque, Japanese monkey, or snow monkey, and is a species native to Japan. Specifically, Japanese macaques range across Honshu, Shikoku, and Kyushu as well as the islands of Awaji, Shodo, Yaku, Kinkazen (Miyagi Prefecture), and Kojima (Miyazaki Prefecture) (Abe et al., 2005). They were also previously native to Tane Island, but have been extirpated (Ibid). Generally, *M. fuscata* prefers two types of habitats – warm temperate evergreen broadleaf forests in the southern section of their geographic range and cool temperate deciduous broadleaf forest in the northern extent of the geographic range (Fooden & Aimi, 2005). Japanese macaques may be found at high elevations, such as the 3050 m Ohamidake mountain, but may also descend to lower elevations during snowy winter months (Ibid). The last assessment for Japanese macaques is dated as 21 November 2015, at which time the IUCN deemed them “Least Concern”, due to both a stable adult population and the absence of significant or severe population fragmentation (Watanabe & Tokita, 2020). As of a 2005 review, the total extant wild population of Japanese macaques was estimated to be approximately 100,000 individuals (Fooden & Aimi, 2005).

Generally, Japanese macaques are medium-sized with pelage color ranging from a pale yellowish-brown to grayish brown to dark golden brown (Fooden & Aimi, 2005) (Fig. 1.1). Individual undergo an annual molt in the late spring/early summer transitioning from relatively long and pale dorsal pelage in the winter to relatively short and dark dorsal pelage in the summer (Ibid). Adult females measure approximated 520 mm in body length and 8.4 kg in body weight while males measure approximately 570 mm in body length and 11.3kg in body weight on average (Fooden & Aimi, 2005) (Fig. 1.2). They are categorized as a semiterrestrial primate and are notable for their affinity for swimming and particularly for their frequent use of natural hot springs particularly in cold winter months (Ibid).

Figure 1.1. Adult male Japanese macaque in winter pelage.

Photo by Kylen N. Gartland

Figure 1.2. Adult male (a) and adult female (b) Japanese macaques.



There are currently two subspecies of Japanese macaque recognized by the IUCN. These include the Japanese macaque (*Macaca fuscata fuscata*) and the Yakushima macaque (*Macaca fuscata yakui*) (IUCN, 2020). The Yakushima macaque is delineated from the common Japanese macaque both in its range, which is restricted to the island of Yaku, and in its morphology. The Yakushima macaque has a smaller overall body size and length than the parent species, has notably darker pelage color on the dorsal surface of the trunk and a blackish color on the dorsal surface of the hands (Fooden & Aimi, 2005).

Wild Japanese macaque populations can also be subdivided based on degree of artificial provisioning. A number of free-ranging groups or populations, notable those inhabiting Kojima, Shodoshima, Takagoyama, and Takasakiyama, receive a significant portion of their dietary requirements from humans (Fooden & Aimi, 2005; Hill, 1999).

Favorable nutritional conditions resulting in low infant mortality tend to result in larger group numbers for provisioned populations (Fooden & Aimi, 2005). To what degree artificial provisioning impacts behavior (and thus may result in behavioral variation between provisioned and non-provisioned populations) is an ongoing question (Hill, 1999).

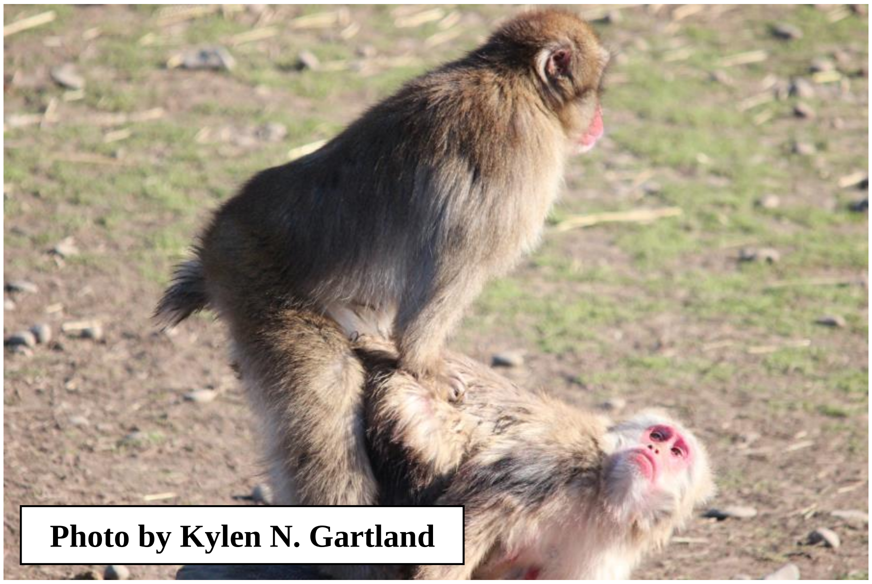
I.VII.I Sociobiology

Japanese macaques are notable as the first wild animals to be individually identified and tracked for an entire lifetime, allowing for the discovering of socially transmitted behavior (Kawai, 1958a, 1958b; Kawamura, 1959). As a result of this long and detailed history of study, the socioecology of free-ranging populations is well established. The average group is a multi-male multi-female social organization of approximately 41 individuals (Fooden & Aimi, 2005; Itani et al., 1963). An analysis of group composition across 35 social groups revealed an approximate split of 18% adult male, 32% adult female, 35% juvenile, and 15% infant (Fooden & Aimi, 2005). Similarly to other macaques, *M. fuscata* create matrilineal, female-bonded groups in which females remain in their natal groups while males over 5 years of age disperse and join new groups (Fooden & Aimi, 2005; Itani et al., 1963; Takahashi, 2002).

Japanese macaques are classified as Grade 1 in dominance style and form highly despotic male and female hierarchies (Adams, Majolo, et al., 2015; Aureli et al., 1993; Chaffin, 1995; Sprague, n.d.; Takahashi, 2002; Kunio Watanabe, 1979). As is typical of matrilineal species with female philopatry, female offspring inherit their rank from their mothers and matrilineal relations. For males, dominance typically forms an inverse-U shaped relationship with age such that both younger and aged males are either low ranked or hold high rank for short durations (Cowlishaw, 1991; Takahashi, 2002). The acquisition of long-term high rank for an adult male may be impacted by any number of environmental or demographic factors. However, it may also be impacted by the continued tenure of previously dominant males such that newly immigrated males may experience a dominance plateau if the current dominant individual(s) do not either emigrate or disappear from the social group (Takahashi, 2002).

While male Japanese macaques may display sexual behaviors while still juveniles, the testes do not descend into the scrotum until approximately 4.5 years of age (Fooden & Aimi, 2005; Soltis et al., 2001; Takahata et al., 2005). Despite reaching physical sexual maturity, and emigrating from the natal group, at approximately 5 years of age, adult males are not fully socio-sexually mature until at least 8.5 years of age. However, this may be accelerated by artificial provisioning. As is common among a number of species, females reach sexual maturity (or at least experience menarche) around 3.5 years of age at which point they also begin displaying estrous behavior (Fooden & Aimi, 2005). *M. fuscata* are generally categorized as multimount ejaculators with each ejaculatory copulation including a series of mounts separated by brief dismounts (Fooden & Aimi, 2005) (Fig. 1.3). Females gestate offspring for approximately 150-170 days before giving birth to a single infant. As with many multi-male multi-female polygynandrous social systems, males have little to no involvement in infant care or rearing (Alexander, 1970; Itani, 1959).

Figure 1.3. Adult male copulating with adult female.



In the discussion of dominance and reproduction, it is important to note a unique departure from the classic model in which dominant males have the greatest reproductive success (de Ruiter, 1993). Namely, this positive correlation between reproductive success and rank has not been consistently observed in Japanese macaques (Eaton, 1974; K. N. Gartland et al., 2020; Inoue et al., 1993; Takahata et al., 2005).

I.VII.II Captive Management

The exact number of Japanese macaques under human management within the United States is not currently known, particularly due to the number of animals that may be held in unaccredited institutions, roadside zoos, or as illegal exotic pets. Additionally, populations of varying sizes are managed in accredited sanctuaries such as the Oklahoma Primate Sanctuary and the Born Free USA Primate Sanctuary in Texas. However, there are much more extensive recordkeeping protocols in place for individuals managed by zoological organizations accredited by the Association of Zoos and Aquariums (AZA) and by National Primate Research Centers (NPRCs). As of the 2016 *Population Analysis and Breeding & Transfer Plan*, there are 129 Japanese macaques under management at AZA facilities with a target population of 175 individuals (Ness, 2016). Across the seven United States NPRCs, only the Oregon National Primate Research Center (ONPRC) currently houses Japanese macaques. The ONPRC houses a single large semi free-ranging multi-male multi-female population of approximately 250 individuals in addition to several smaller one-male units with individuals used for current biomedical research. The exact structure, housing, and care of the ONPRC populations will be discussed in Chapter II.

Many organizations managing Japanese macaque populations construct social units in a way which represents significant departure from the natural social group organization. Namely, many populations are significantly smaller than the average *ex situ* social group and may be formed and maintained as one-male units rather than as multi-male multi-female social groups (Ness, 2016, 2018).

Some aspects of socioecology vary between captive and wild populations. Dominance, particularly in the ONPRC Japanese macaques, is significantly related to age such that older males are often more dominant than younger males (K. N. Gartland et al., 2020; Johnson, 1982). Additionally, males display more paternal behavior or directed affiliation with juveniles than that observed in wild populations (Alexander, 1970; K. N. Gartland et al., 2020). This affiliative behavior can include ventro-social huddling (Figure 1.4), protective behavior (Figure 1.5), or carrying (Figure 1.6).

Figure 1.4. Adult male Japanese macaque ventro-social huddling with immature.

Photo by Kylen N. Gartland

Figure 1.5. Adult male Japanese macaque protecting immature clinging to ventral.

Photo by Kylen N. Gartland

Figure 1.6. Adult male Japanese macaques carrying immatures.

Photos by Kylen N. Gartland

I.VII.III Management Tools and Welfare Applications

A number of methods for addressing socioecological questions in wild populations have been adapted for use in captive populations. Adapting methodology from field studies allows both for comparisons of wild *versus* captive socioecology as well as identification of strategies for successful management and improved welfare of captive populations. At the most basic level, the standard methods of behavioral observation used widely across both field and captive settings (Altmann, 1974) have been used across a wide variety of taxa to examine an array of welfare questions. Captive institutions have used this sampling methodology to examine behavioral outcome and welfare measures across any number of situations including social housing conditions (Kuhar, 2008; Stoinski et al., 2013), major group transitions (Doyle et al., 2008; Gartland et al., 2018; Seres et al., 2001), or significant veterinary procedures (Coleman et al., 2011). Often, behavioral sampling is a means of obtaining data for analyses with more concrete welfare implications.

For example, behavioral data may be used to establish a dominance matrix for use in a David's Score analysis (Gammell et al., 2003). A David's score may elucidate dominance relationships between individuals or entire hierarchies, which can inform decisions pertaining to group formation and strategies for mitigation of aggression (McCowan et al., 2008).

Social network analysis has also been especially prevalent as a tool in captive management. Applications of social network theory and social network analyses have allowed captive institutions to strategically identify ideal group formations, locate sources of social instability, and examine the roles that single individuals may play in larger group cohesion (Beisner et al., 2011; McCowan et al., 2008; McCowan & Beisner, 2017; Wey et al., 2008).

While examining behavioral or socioecological questions from a theoretical perspective may grant insight into questions of evolution or conservation, examinations of behavior itself can also elicit important benefits from a management perspective as well. As such, studies of behavior within captive populations are frequent and highly utilized within the zoological field.

I.VIII Hypotheses

The overarching goals of this study are broadly to examine male sociality in Japanese macaques and specifically: (1) examine dominance and network centrality as management tools; (2) evaluate differential behavioral strategies among adult males; and (3) to assess the relationship between sociality trends, focal male demography, and social partner demography. Based on the preceding review of socioecology, evolutionary theory, and known Japanese macaque behavior, I have formulated the following hypotheses:

Dominance and Centrality: Chapter III

Hypothesis 1: If dominance is consistent across contexts, hierarchies produced from different statistical analyses should show insignificant variation.

Hypothesis 2: If dominance selects for social skills, then dominant adult males should also be highly central within the male social network.

Behavioral Strategies – Chapter IV

Hypothesis 1: If aggression is the most effective behavioral strategy for adult males, then males with high directed aggression should be the highest rank and have the highest reproductive success.

Hypothesis 2: If affiliation is the most effective behavioral strategy, then males with high rates of bi-directional affiliation should attain both high rank and high reproductive success.

Hypothesis 3: If alternative mating strategies are effective within this population, we should see a complex individualistic relationship between rates of aggression, affiliation, rank, and reproductive success.

Biological Market Strategies – Chapter V

Hypothesis 1: If adult males who hold high rank also hold central positions within biological markets, then these individuals can limit their exerted social energy. This will be reflected in their degree of sociality and type/number of social partners.

Hypothesis 2: If younger adult males have less central positions within the biological market, then these individuals must exert higher social effort to secure trading partners. This will be reflected in their degree of sociality and type/number of social partners.

CHAPTER II

METHODS

II.I Study Population

As mentioned in Chapter I, the Oregon National Primate Research Center (ONPRC) is home to the largest research-accessible population of Japanese macaques (*Macaca fuscata*) in human care. The ONPRC currently houses two types of social groups – a single large multi-male multi-female population (hereafter referred to as the primary troop) and a number of one-male units. These one-male units are collectively referred to as extra-troop harem groups. For the purposes of this study, we only observed the primary troop. This population was established at the ONPRC in 1964. The original troop members, and genetic ancestors of the current group members, were donated to the ONPRC by the Japanese government. This particular group had become threatened in their native Japanese range due to deforestation and human-wildlife conflict (*Caring for Our Animals*, 2020). As such, the group was donated to the ONPRC for conservation and research purposes with a special focus on behavior and social organization. Later investigations revealed that the Japanese macaques serve as natural models for biomedical research into multiple sclerosis, age-related macular degeneration, and Batten disease (*Caring for Our Animals*, 2020).

Following their arrival at the ONPRC, the Japanese macaques have been the focus of a number of primatological studies, most notably by researcher G.G. Eaton. Studies on this population have covered a range of topics including paternal behavior, behavioral seasonality, ovariectomies, dominance, various elements of social organization, and sex-based differences (Alexander, 1970; Alexander & Bowers, 1967; Coleman et al., 2011; Eaton, 1972, 1974, 1976, 1978; Eaton et al., 1981, 1985, 1986; K. N. Gartland et al., 2020; Gottlieb et al., 2017; Hanby et al., 1971; Johnson, 1982; Rostal et al., 1986).

Social organization and overall structure within this population largely mirrors what has been reported for wild populations (see Section I.VIII). The group is multi-male multi-female with a polygynandrous mating system. This troop displays some characteristics of a despotic system – notably a highly linear hierarchy present in both sexes (see Chapter III). There is limited emigration within this population, largely facilitated by management. Some individuals, usually a single adult male and a small selection of adult females, are removed yearly for the creation of one-male units. These one-male units are formed for the purpose of biomedical research and cultivation of the natural models mentioned above.

Juveniles, usually yearlings, from the extra-troop harem units are routinely re-integrated into the original larger population (K.Coleman, pers. comm.). Although these extra-troop integrated juveniles have extended biological relatives within the primary troop, their separation from the primary troop at birth has resulted in disconnection from their genetic maternal hierarchy.

Otherwise, there is no immigration of genetically unconnected individuals into the primary troop and has been no new genetic material added to the population since the arrival of the original troop in 1964.

II.I.I Housing

This population has been referred to as living in a semi free-range habitat or a seminatural habitat. The troop has much more restricted human interaction than is typically characterized by traditional captive environments such as that found in zoological organizations. The troop has been habituated to human observation, which primarily occurs from one of two observation towers. Observation towers are located outside of the perimeter of the corral, but placed so as to overlook the enclosure. The troop has minimal reaction to the presence of visitors or observers. Visitors may be present intermittently throughout the year, though are usually sporadic and contained to small groups. The largest human presence comes from scheduled group tours which happen on a small number of occasions from approximately June to September.

However, the troop does register the presence of corral technicians, likely because the corral technicians provide daily high-value enrichment foods. Troop members frequently vocalized upon the arrival of corral technicians at the observation towers and would gather below the towers for dispersal of enrichment. The corral technicians also enter the corral two or three times weekly for the purpose of small repairs and medical observations. On these occasions, the macaques are highly avoidant of the technicians and high-ranking adult males may display aggressively at the technicians. The macaques are also resistant to the sporadic captures for veterinary intervention or bi-annual processing and check-ups. As such, the population as a whole has retained the more wild-typical human avoidance behaviors such as might be seen in both provisioned and non-provisioned wild populations.

However, unlike the traditional semi free-ranging provisioned troop, the ONPRC population is housed in an enclosed corral. The outdoor portion of the enclosure measures one square acre and is surrounded by high steel walls. In addition to the outdoor corral, the group has constant access to an indoor feeding room which measures approximately 3 x 12 meters. The only times this room is closed to the macaques is when it is being cleaned by technicians or when technicians have entered the corral for medical intervention.

The outdoor corral is equipped with platforms and structures of varying heights and design for the purpose of play and enrichment. There are also sprinklers placed around the corral which are activated on particularly hot (>80 degrees F) days during the summer and early fall. Although this species is endemic to high altitude and cold weather, weather in Beaverton, Oregon is significantly milder than that in the mountains of Japan.

The group is primarily fed a diet of commercial monkey chow which is provided twice daily by corral technicians. In addition to monkey chow, the macaques' diets are supplemented with high-value enrichment included a diverse array of fruits, vegetables, and grains. Different enrichment items have varying preferential worth to the macaques, resulting in differential access based on social status. The most high-value items for this population include bananas, melon, and grapes. Water is available ad libitum from multiple spigots along one wall of the enclosure.

II.I.II Group Composition

As noted in Section I.VIII.I, the average wild Japanese macaque population contains approximately 41 individuals (Fooden & Aimi, 2005). However, group size can be highly variable and grow as large as 180 individuals, likely depending on range and food availability (Takasaki, 1981). The ONPRC primary troop fluctuates in size but often ranges between 200 and 250 total individuals (Table 2.1).

Table 2.1. ONPRC Primary Troop Composition in 2018 and 2019

	2018		**2019**	
Age-Sex Class	**#**	**%**	**#**	**%**
Adult Male	16	7.2	15	6.1
Adult Female	60	27.1	89	36.3
Subadult Male	8	3.6	23	9.4
Juvenile Male	62	28.1	51	20.8
Juvenile Female	70	31.7	55	22.4
Infant	5	2.3	12	4.9
Total	221		245	

While sociosexual maturity happens in wild populations at around 8.5 years of age for males and 3.5 years for females, provisioning has decreased the time for sociosexual maturity (K. Coleman, pers. comm.; Fooden & Aimi, 2005). As such, the age classifications used for the ONPRC population are as follows: infants (<1 year), juveniles (1 to 4 years), subadult male (>4 to 7 years), adult female (>4 to 15 years), adult male (>7 to 15 years), and aged individuals (>15 years). These age classifications were provided by K. Coleman at the ONPRC and were only slightly modified for use in this study. For example, based on the wild data on sociosexual maturity as well as personal observations of body size and social behavior, we did not include a subadult classification for females. We also separated the previously encompassing “infant” category into “infant” and “juvenile” which arose from observations of male-initiated affiliation (K. N. Gartland et al., 2020).

An analysis of group composition across 35 wild social groups revealed an approximate split of 18% adult male, 32% adult female, 35% juvenile, and 15% infant (Fooden & Aimi, 2005). In comparison, the ONPRC population distribution is weighted more heavily towards juveniles particularly. If we combine the subadult and adult male categories, then we find a compositional distribution of 10.8% adult male, 27.1% adult female, 59.8% juvenile, and 2.3% infant for the ONPRC in 2018 (Table 2.1). The compositional distribution for the ONPRC 2019 was 15.5% adult male, 36.3% adult female, 43.2% juvenile, and 4.9% infant.

II.I.III Study Subjects

For the purposes of this study, only males aged 7 years or older or males who reached 7 years of age during one of the two study periods were included in behavioral sampling. Subjects ranged from 7 to 25 years of age (Table 2.2). Males were separated into two age categories: adult (>7 to 15 years) and aged (>15 years). This allowed for extra investigation into age-related effects on sociality and a focus on the comparison of behavior across individuals either within or reaching their physiological prime and individuals past their physiological prime.

Table 2.2. Individual subject identification, age class, and age across 2018 and 2019

	Age Class		**Age**	
Identification	**2018**	**2019**	**2018**	**2019**
AM1	Aged	*Deceased*	25	*Deceased*
AM2	Aged	Aged	21	22
AM3	Aged	Aged	20	21
AM4	Aged	*Deceased*	18	*Deceased*
AM5	Aged	Aged	17	18
AM6	Adult	*Removed*	9	*Removed*
AM7	Adult	Adult	10	11
AM8	Adult	Adult	8	9
AM9	Adult	Adult	8	9
AM10	Adult	Adult	8	9
AM11	Adult	Adult	8	*Removed*
AM12	Adult	Adult	9	10
AM13	Adult	Adult	8	9
AM14	Adult	Adult	6	7
AM15	Adult	Adult	7	8
AM16	*Subadult*	Adult	6	7
AM17	*Subadult*	Adult	6	7

Some individuals were only present for one of the two data collection periods due to age, death, or management removal for creation of extra-troop harems. AM1 died on October 25, 2018 as a result of age-related health complications. AM4 died on October 17, 2018 as a result of age-related health complications. AM6 was removed on October 10, 2018 for placement in an extra-troop harem. AM11 was removed on February 15, 2019 for placement in an extra-troop harem. AM16 and AM17 were subadults during the initial 2018 study period, but aged into the study for the 2019 data collection. It is also worth noting that AM3, who was identified by corral technicians and members of the ONPRC Behavioral Science Unit as the dominant male, died in summer 2020. Reports from the ONPRC suggest that he was replaced as dominant male by AM8.

The adult male study subjects were individually identifiable by pelage or facial features as well as dye-markings on their backs. Markings included a large number central on their back as well as dye on a combination of their right and/or left limbs. Every individual, excluding infants, was dye-marked in this way. Individuals who had been born in extra-troop harems and integrated as yearlings also had black dye on their skulls to make them identifiable. Individuals are processed twice yearly for veterinary check-ups and renewed dye-markings.

Only one available adult male within the primary troop was excluded from the study. The combination of this young adult male's small size and tendency to quickly groom off or otherwise rid himself of his identifying dye-markings made him indistinguishable from subadult males within the troop. This individual was never reliably identified by all observers, resulting in few and inconsistent data. As a result, he was removed from the study.

II.II Behavioral Observations

We conducted 15-minute focal follows of individuals using 1-minute instantaneous scans (Altmann, 1974). Data were collected from approximately 08:30 to 16:00 Mondays through Fridays. Observers did not have access to the ONPRC outside of these days and time periods, which restricted available observation hours. This span of daily time allowed for approximately 20 focal follows to be conducted per day with breaks in observation between follows. This arrangement allowed for each observer to conduct 1-2 focal follows per subject per day. Focal order was randomly selected. If a focal individual was unavailable for a follow, usually due to being out-of-sight within the feed room, then the observer moved on to the next individual on the list and returned to the unavailable focal individual at the earliest possible time. Observations were conducted from the observation towers. All observers were equipped with a clipboard and printed focal data sheets (Appendix A), a pair of Nikon Aculon A211 binoculars, a Timex IronMan watch for tracking scan intervals, an identification guide to the study subjects, a focal tracker, and a copy of the ethogram.

II.II.I Ethogram

The ethogram for this study was designed to be address questions of sociality (Table 2.3). Although an array of solitary behaviors were included in the ethogram, sociality was expanded to be as comprehensive as possible. As such, social behaviors were split into three behavioral classes including social (SOC), agonistic (AGG), and socio-sexual (SOS) (Table 2.3).

Ideally all social, agonistic, and socio-sexual behaviors included recording of data pertaining to their interaction partner. This recorded data included the partner’s individual identification, age-sex classification, and whether the individual was natal to the primary troop or had been integrated from one of the extra-troop harems. Finally, we recorded which individual(s) initiated or terminated a given social interaction. Initiation and termination were only recorded if observed during the focal follow. To avoid biasing in sampling, social interactions that continued after the 15-minute focal period were not recorded to termination. Individual identification of social partners was not always possible as a result of factors including rapid movement, brevity of interaction, or obscuring/absence of identifying dye-markings. If social partner was not reliably identified, observers still recorded age-sex classification. Finally, observers also noted directionality of social behaviors (give *versus* receive) relative to the focal individual.

Table 2.3. Ethogram

Behavioral Class	Behavior	Definition
Social (SOC)	Groom (GM)	Manipulation of the hair of another individual (s) with hand and/or mouth
	Play (PL)	Social interactions that are characterized by apparent low tension; may be accompanied by a "play face" (facial gesture in which mouth is open and facial features are relaxed). May include any of the following: grunting, wrestling, sham-biting, jumping on, jumping over, chasing, fleeing, hiding.
	Huddle (HO)	Subject is in physical contact with another individual(s), including huddling.
	Ventral Contact (VC)	Focal individual gives ventral contact to at least one other individual.
	Other (OT)	Subject is engaged in behavior not listed in Ethogram; describe in comments section of observation sheet
Agonistic (AGG)	Chase (CH)	Behavior that involves pursuit past the location the recipient maintained at the start of the interaction.
	Threat (TH)	Expression containing facial, vocal, or physical components (may include head thrusting, open-mouth threat, scream, raised eyebrow, ground beating, lunge).
	Bite (BI)	During which the skin/limb of another animal is grasped with the teeth; may be accompanied by head shaking.
	Contact (CO)	May include nipping, grabbing, kicking, pulling, pushing, poking, slapping, pulling hair, butting, shoving.
	Flee (FL)	Focal individual runs from an aggressor
	Other (OT)	Subject is engaged in other form of aggressive behavior not covered by the above categorizations.
Socio-Sexual (SOS)	Mount (MO)	Subject mounts another individual.
	Copulate (CO)	Subject engages in copulation with another individual.
Solitary (SOL)	Abnormal (AB)	Subject is engaged in atypical behavior; may include any of the following: stereotype, self-bite, copraphagy, floating limb.

Table 2.3. Ethogram, continued

Behavioral Class	Behavior	Definition
	Eat (EA)	Subject is ingesting liquid (drinking) or solid food material (common usage).
	Explore (EX)	Subject inspects or manipulates object other than food.
	Forage (FO)	Subject is searching through grass or other substrate material, presumably for food.
	Locomotion (LO)	Subject engages in movement from one location to another while using its entire body.
	Self-Groom (SG)	Picking through and/or slowly brushing aside own hair with hands and/or mouth.
	Self-Play (SP)	Subject engages in independent play with active movement; may include swinging, running, or spinning on objects.
	Stationary (ST)	Subject is inactive without motile movement; may still involve head or arm movement. Also includes sleeping.
	Other (OT)	Subject is engaged in behavior not listed in Ethogram; describe in comments section of observation sheet.
Out of View (OV)		Individual is out of observer view. Do not record partner.

During study Period III (discussed below in section II.II.II), observers recorded copulations on an all-occurrence basis using a tally count. It is important to note that due to extenuating circumstances at the ONPRC, the group was not processed in October 2019 as is usual. As such, most of the identifying dye-markings had faded or been fully groomed out. Identification of focal individuals and social partners was delayed during this time period, resulting in less gathered hours of data per day spent at the ONPRC.

II.II.II Study Periods

Data collection was split into three distinct study periods. Period I spanned from June 27th to September 29th of 2018. During this initial study period, all data were collected by K.N.G. Period I resulted in a total of 154 hours of recorded data across 39 days spent at the ONPRC. Period II spanned from July 4th to September 20th of 2019. During this period, data were collected by K.N.G. and undergraduate research assistants C.M.S. and N.B. C.M.S. and N.B. were trained by K.N.G. for a period of approximately six months beginning in January 2019. Data collection did not begin until interobserver reliability had been established with a minimum score of 85% consistency across observers. Interobserver reliability was established on July 3rd 2019, and then retested in August 2019 to confirm that reliability had remained constant. Period II resulted in a total of 320.5 hours across 52 days spent at the ONPRC. Finally, Period III spanned from October 4th 2019 to March 3rd 2020. During this period, all data were collected by C.M.S. Visitation at the ONPRC was more intermittent, as observer C.M.S. was only able to visit once weekly due to academic commitments. Period III was intended to continue through June 2020 and lead directly into Period IV which would have spanned approximately June through September 2020. However, the spread of the COVID-19 pandemic resulted in loss of access to the ONPRC for all members of this project starting in March 2020. Period III was cut short and it was not possible to collect data for Period IV. The abbreviated Period III resulted in 38 hours across 19 days spent at the ONPRC.

Data collection Periods I and II largely overlapped with the birthing season, which usually ranges from May to August at the ONPRC. The largest number of births usually occurs in June and July (K. Coleman.; pers. comm.).

II.II.III Data Hours Summary

Observers endeavored to collect equal hours of behavioral data across all study subjects within study periods. A summary of data hours by study period and separated by focal individual is presented below (Table 2.4).

Table 2.4. Data Hours by Focal Individual and Study Period

Focal	Data Hours				Focal Follows			
	Period I	**Period II**	**Period III**	**Total**	**Period I**	**Period II**	**Period III**	**Total**
AM1	11	0	0	11	44	0	0	44
AM2	11	24.75	2.75	38.5	44	99	11	154
AM3	11	24.5	2.5	38	44	98	10	152
AM4	11	0	0	11	44	0	0	44
AM5	11	24.75	3	38.75	44	99	12	155
AM6	11	0	0	11	44	0	0	44
AM7	11	24.75	3	38.75	44	99	12	155
AM8	11	24.5	3.25	38.75	44	98	13	155
AM9	11	24.75	2.75	38.5	44	99	11	154
AM10	11	24	2.5	37.5	44	96	10	150
AM11	11	0	0	11	44	0	0	44
AM12	11	24.5	2.25	37.75	44	98	9	151
AM13	11	25	2.75	38.75	44	100	11	155
AM14	0	24.75	3	27.75	0	99	12	111
AM15	11	24.75	2.5	38.25	44	99	10	153
AM16	0	24.25	3	27.25	0	97	12	109
AM17	0	25	3.25	28.25	0	100	13	113
Total	154	320.5	38	512.5	616	1281	152	2049

II.III Fitness Data

During the bi-annual processing of the primary troop conducted by ONPRC management, each individual undergoes a routine medical examination. This examination, performed while the animals are sedated, includes a weight recording, assessment of vitals, and extraction of a small sample of blood for testing. In the case of infants born since the previous testing, the examination also includes extraction of a small sample for genetic testing. This is also when individuals are tattooed with their 5-digit identification numbers and given fresh dye-marks.

The genetic testing allows for ONPRC management to track genetic lineages in order to select optimum individuals for extra-troop harem formation and to monitor levels of inbreeding within the population. Genetic testing also establishes paternity. Paternity data, up to date as of May 2018, were provided by the ONPRC. Due to delayed processing and impediments caused by the COVID-19 pandemic, updated paternity data for infants born after May 2018 were not available.

The provided paternity data allowed us to establish: 1) how many offspring each male had as of May 2018, 2) the age and sex of each offspring, 3) the age at which the focal male fathered each offspring, and 4) the genetic mother of each offspring. These data were then used in analyses pertaining to reproductive success. The fitness data as provided by the ONPRC are summarized below (Table 2.5).

Table 2.5. Summary of reproductive success data updated as of May 2018.

Sire	Offspring Sex	Birth Year	Male Age at Siring (yrs)
AM1	Female	2001	7
AM1	Female	2001	7
AM1	Female	2005	11
AM1	Female	2015	21
AM2	Female	2015	17
AM2	Female	2015	17
AM2	Female	2016	18
AM3	Female	2004	5
AM3	Male	2017	19
AM4	Female	2006	5
AM4	Male	2015	15
AM4	Female	2015	15
AM4	Male	2015	15
AM4	Female	2015	15
AM4	Male	2017	17
AM5	Female	2014	13
AM5	Female	2014	13
AM5	Male	2016	15
AM5	Male	2016	15
AM5	Female	2016	15
AM6	Male	2016	8
AM6	Female	2016	8
AM6	Male	2017	9
AM6	Male	2017	9
AM7	Male	2015	6
AM7	Male	2015	7
AM7	Female	2016	7
AM7	Female	2016	7
AM7	Female	2016	7
AM7	Female	2017	8
AM8	Female	2016	6
AM8	Male	2016	6
AM8	Male	2016	6
AM8	Female	2016	6
AM8	Female	2016	6
AM8	Female	2016	6
AM8	Male	2017	7
AM8	Female	2017	7
AM8	Male	2017	7
AM8	Female	2017	7
AM8	Female	2017	7
AM9	Female	2015	5
AM9	Male	2015	5

Table 2.5. Summary of reproductive success data, continued

Sire	Offspring Sex	Birth Year	Male Age at Siring (yrs)
AM9	Male	2015	5
AM9	Male	2016	6
AM9	Female	2016	6
AM10	Female	2015	5
AM10	Female	2017	7
AM10	Female	2017	7
AM10	Female	2017	7
AM11	Male	2017	7
AM11	Female	2017	7
AM12	Male	2015	5
AM12	Male	2016	6
AM12	Male	2016	6
AM12	Male	2016	6
AM12	Female	2017	7
AM12	Female	2017	7
AM12	Female	2017	7
AM12	Male	2017	7
AM12	Female	2017	7
AM12	Female	2017	7
AM13	Male	2016	6
AM13	Male	2017	7
AM14		*Data Unavailable*	
AM15	Male	2017	6
AM15	Female	2018	6
AM16		*Data Unavailable*	
AM17		*Data Unavailable*	

II.III. Bridge to Chapter III

The purpose of this chapter was to broadly review the methodology for this dissertation. As described in this chapter, data were collected during multiple study periods across a sample size that fluctuated as a result of naturally-occurring deaths and management decisions made by ONPRC staff. A full overview of the dataset, particularly observation hours per individual and fitness data, is presented here as all data were not used in every chapter. For example, fitness data is not included in analyses for Chapter V.

Data analysis varied distinctly across chapters, and so was not summarized here but is reviewed in depth within each core chapter (Chapters III, IV, and V).

CHAPTER III

STABILITY OF DOMINANCE ACROSS TIME AND CONTEXT IN ADULT MALE JAPANESE MACAQUES (*MACACA FUSCATA*): IMPLICATIONS FOR GROUP MANAGEMENT

This chapter includes material which is currently under review for publication with the Journal of Applied Animal Welfare Sciences. *Material is reproduced with permission from Gartland, K.N., Shreeve, C.M., Biggs, N. and White, F.J. The author, Kylen N. Gartland, was the principle investigator for this work and is responsible for designing the study, behavioral data collection, statistical analyses, and manuscript preparation. Frances J. White is the graduate advisor for this dissertation and participated in study design, statistical analysis, and manuscript review. Nichole Biggs and Caitlin M. Shreeve are undergraduate research assistants who participated in data collection, statistical analyses, and manuscript preparation.*

III.I Introduction

Social network analysis seeks to assess relationships within a social group through a variety of measures, usually focusing on centrality which assesses an individual's importance within a social group based on their relative position within a larger network (Wey et al., 2008). The most relevant individual measures are degree, betweenness, closeness, and eigenvalue. Within social network theory, degree is defined as the number of direct connections an individual has (McCowan & Beisner, 2017; Wey et al., 2008). Closeness largely measures the minimum distance between a focal individual and other individuals in the network. Closeness is unique in that it accounts for both direct and indirect connections (McCowan & Beisner, 2017). Betweenness measures the degree to which individuals are positioned on pathways connecting other pairs of individuals in the network and thus are fundamental in maintaining group cohesion (McCowan & Beisner, 2017; Wey et al., 2008). Finally, eigenvalue compares an individual's degree centrality against that of its neighbors or other individuals in the network. Many of these measures are often correlated, as individuals with high degree measures are likely to also have high closeness and betweenness (McCowan & Beisner, 2017).

Networks are constructed to allow for analysis based on individuals and generalized demographic factors such as age, sex, rank, or lineage (McCowan & Beisner, 2017; Wey et al., 2008). An individual may have many direct social partners within a single network or indirect connections through a mutual third-party (Brent et al., 2013). This approach can allow for evaluating not only direct dyadic relationships between dominant and subordinate individuals, but also investigations from a more global group perspective into the relative positionality and necessity of particular individuals to the stability and character of the social group (Makagon et al., 2012). These metrics enable identification of individuals who may play critical, but subtle, roles in group stability.

Social groups are characterized by competition for resources including food, territory, and reproductive opportunities (Moosa & Ud-Dean, 2011). Dominance is differential access to these resources and often arranged in a hierarchy such that higher ranked individuals have primary access to resources, often resulting in increased reproductive fitness (Bernstein, 1976). Dominance can be attained or measured through a number of factors including lineage, age, social competence, reproductive success and fighting ability (Chaffin, 1995; Cooper & Bernstein, 2008; Flack & de Waal, 2004; Hinde, 1976). Dominance hierarchies have been assessed from multiple perspectives, though often focus on some form of affiliative or aggressive dyadic behavioral interaction (Bernstein, 1976; Cooper & Bernstein, 2008; De Vries, 1998; De Vries et al., 2006). For example, grooming directionality has been used as an indicator of rank in Japanese macaques (*Macaca fuscata*) such that males that received more grooming, particularly from other adult males, were deemed higher ranking than those who primarily direct grooming at other individuals (Cooper and Bernstein 2008). Rank within a hierarchy can be heavily influenced by the relationships made within the social group. Both the form and the degree of importance of dominance can be highly variable depending on social structure.

Stability is maintained through an organized social structure which is maintained through dyadic relationships (Balasubramaniam et al., 2012). Affiliative interactions between dyads serve to strengthen bonds whereas agnostic behaviors reinforce the existing hierarchy (Ostner & Schülke, 2014b). The frequency and strength of affiliative bonds, particularly between adult males, is highly dependent on social structure. Macaque species are socially categorized along a spectrum ranging from tolerance to despotism in which tolerant groups are characterized by loose hierarchies or egalitarian dominance, high reconciliation, and low severity of aggression whereas despotic systems are characterized by steep linear hierarchies, little reconciliation, and intense aggression (B. Thierry, 2000).

Studies of provisioned semi free-ranging rhesus macaques (*Macaca mulatta*) have previously demonstrated how intersection of both dominance and social network analysis can provide captive management insight (Beisner et al., 2011; Makagon et al., 2012;

McCowan et al., 2008, 2011; McCowan & Beisner, 2017). Social network measures can be significantly associated with rates of contact aggression, wounding, and aggressive outbreaks (McCowan et al., 2008). Researchers also found that social network measures could be used to track changes in dynamics and stability within the group longitudinally, allowing for preemptive management action (Ibid). Another study reported that individual personality characteristics, which necessarily encompass degree of dominance, influence network structures and can act as indicators of network robustness in rhesus macaques (McCowan et al., 2011). However, it is important to note that these studies have been singularly focused on the highly despotic rhesus macaque.

Japanese macaques (*Macaca fuscata*) are one of the three most prominent macaque species in captivity and biomedical research (Chaffin, 1995). While classified as despotic in wild populations, there has been debate over whether environmental factors such as those found in captivity may influence a more tolerant social structure (K. N. Gartland et al., 2020; Lunardini, 1989; Schino et al., 2005; Zhang & Watanabe, 2014). As species-typical behavior and social structure can vary significantly even within a single genus such as *Macaca*, generalizations based on rhesus macaque models cannot be applied to Japanese macaques. In this study, we propose to demonstrate the utility of social network analyses in partnership with dominance and hierarchical assessments as tools in the management of multi-male Japanese macaque social groups in captivity.

III.II Methods

III.II.I Study Subjects and Location

This study was conducted on the population of Japanese macaques at the Oregon

National Primate Center in Beaverton, Oregon, USA. This population is a semi-free ranging group housed in a one square acre outdoor corral equipped with an indoor feeding room measuring three meters by 12 meters. Inside the corral, there were a number of platforms and toys for play and enrichment. Outside the corral, there were two observation towers for staff and research personnel. This group was fed a diet of commercial monkey chow along with enrichment foods such as fruits vegetables and grain. Each individual was given unique dye mark using animal-safe cattle dye which allowed identification from the observation tower. At the initiation of the study in June 2018, the social group included 221 individuals which fluctuated over the study period to over 250 individuals. Only including adult individuals, this group has a male to female sex ratio of approximately 1:3. Only male individuals classified as adult (>7 to 15 years) or aged (>15 years) following the age classifications provided by the ONPRC were included in the study (K. Coleman, pers. comm.) (Table 3.1).

III.II.II Data Collection

We collected data during two distinct time periods: June – September 2018 and July – September 2019 (Table 3.1). Authors K.N.G (2018 and 2019), C.M.S. (2019) and N.B. (2019) were responsible for data collection. With the addition of observers C.M.S. and N.B. in 2019, all observers were tested for inter-observer reliability and maintained a minimum of 80% agreement throughout data collection.

TABLE 3.1. Study subjects, ages, ranks, and hours of observation.

Individual	Age (years)	Age-Class	Data Hours 2018	Data Hours 2019
AM1	25	Aged	11	*Deceased*
AM2	21	Aged	11	25.75
AM3	20	Aged	11	25.5
AM4	18	Aged	11	*Deceased*
AM5	17	Aged	11	26
AM6	9	Adult	11	*Removed*
AM7	10	Adult	11	26
AM8	8	Adult	11	26
AM9	8	Adult	11	25.75
AM10	8	Adult	11	25
AM11	8	Adult	11	*Removed*
AM12	9	Adult	11	25.5
AM13	8	Adult	11	26
AM14	7	Adult	11	25.75
AM15	7	Adult	11	25.75
AM16	6	Sub-Adult	*Immature*	25.5
AM17	6	Sub-Adult	*Immature*	26.5

*Age and age-class presented as of June 2018.

We collected data using 15-minute focal follows according to well-established methodology and previous protocol within this particular longitudinal project (Altmann, 1974; K. N. Gartland et al., 2020). However, we made small adjustments to the data collection protocol established in 2018 such that instantaneous sampling occurred at one-minute intervals in 2019 but 30-second intervals in 2018. In order to maintain consistency in analyses, we condensed the 2018 data set so as to have one-minute interval data for all individuals throughout the study. Our data collection resulted in a total of 475 hours spread over 17 individuals. We recorded data following a pre-determined ethogram which was consistent across both the 2018 and 2019 study periods. This ethogram emphasized social behaviors, particularly both contact and non-contact forms of aggression and affiliation. Recorded behaviors relevant to these analyses included grooming, playing, huddling, ventral contact, chasing, threat, biting, non-biting aggressive contact, fleeing, submitting, and ignoring. For all social interactions, we recorded the directionality of the behavior (whether the focal individual was the recipient or director of behavior), the age and sex class of the social partner, and social partner identification. In some cases, individual identification of social partner could not be made due to visual obstruction of the body and/or dye markings or fading of dye markings. However, all adult male subjects could be reliably identified at a distance without the aid of dye markers.

III.II.III. Data Analysis

In order to conduct reliable and consistent analyses across time, only individuals present for both the 2018 and 2019 study were included in dominance and social network analyses. Males AM1 and AM4 died of natural causes between the study periods, and thus were not included. Individuals AM6 and AM11 were removed from the primary social group as center males for new one-male units elsewhere on the ONPRC campus after the 2018 study period and thus not included. Finally, individuals AM16 and AM17 were sub-adults at the outset of the 2018 study and thus were only included in data collection for the 2019 period. Of the total 17 males in the study, this left us with 11 subjects for these analyses. We assessed dominance rank through two approaches. The first was a categorical (high, middle, low) rank assignment based on opportunistic observations of priority-of-access to high value food enrichment, precedence for which was established in 2018 (K. N. Gartland et al., 2020). Priority-of-access observations often occurred outside of focal follows, as the schedule maintained by ONPRC was somewhat unpredictable. The second approach was David’s Score analyses, which use win/loss matrices of social interactions to create linear rankings (De Vries, 1998; De Vries et al., 2006). In total we calculated separate rankings for 2018 and 2019 using the categorical approach, David’s Score analyses based on aggressive interactions, and David’s Score analyses based on grooming interactions. After constructing these hierarchies, we ran analyses of variance (ANOVAs) to test for significant variation in individual rank between the hierarchies and for significant variation in individual rank between years. In order to compare across hierarchies, the David’s Scores hierarchies were converted to a categorical classification with the four highest ranking individuals classified as “high”, the next four individuals classified as “middle”, and the three lowest ranking individuals classified as “low”.

We then used affiliative interactions between the adult males to create a social network of the adult males in order to investigate both their relationships to each other and their centrality to the dominance hierarchy. We calculated degree, betweenness, closeness, and eigen value for each male for 2018 and 2019. We chose to investigate these measures as we believed they would provide the most comprehensive indicators of individual position within the male network and thus their importance to the stability of the existing hierarchy. We ran a second set of ANOVAs to examine variation in closeness and betweenness both between individuals and between years. We then ran GLMMs (generalized linear models) to investigate a possible relationship between 1) closeness, categorical rank, and year; and 2) betweenness, categorical rank, and year. We ran Pearson's correlations to look for significant relationships between both closeness and rank and betweenness and rank for 2018 and 2019.

III.III. Results

Dominance analyses resulted in three separate hierarchies for both 2018 and 2019 (Tables 3.2, 3.3, and 3.4). The 2018 grooming-based David's Score analyses resulted in three individuals (AM5, AM9, and AM12) having equal rank (Table 3.2). There was significant variation in both the normalized David's Scores (F=22.76, df=1, p=0.001) and resulting rank assignments (F=38.37, df=1, p < 0.001) between 2018 and 2019.

TABLE 3.2. Grooming-Based David's Score Analysis Results for 2018 and 2019

ID	2018 David's Score	2018 Rank	2018 Categorical Rank	2019 David's Score	2019 Rank	2019 Categorical Rank
AM2	0.77	3	High	0.39	3	High
AM3	0.82	2	High	0.45	2	High
AM5	0.53	5	Middle	0.30	5	Middle
AM7	0.00	9	Low	0.00	11	Low
AM8	1.00	1	High	1.00	1	High
AM9	0.53	5	Middle	0.25	7	Middle
AM10	0.65	4	High	0.26	6	Middle
AM12	0.53	5	Middle	0.32	4	High
AM13	0.24	8	Low	0.21	8	Middle
AM14	0.35	7	Low	0.15	9	Low
AM15	0.41	6	Middle	0.06	10	Low

The very low number of observed aggressive interactions between adult males resulted in a largely empty interaction matrix for the aggression-based hierarchy. As a result, there were six individuals (AM3, AM9, AM10, AM13, AM14, and AM15) tied for rank position three and three individuals (AM4, AM7 and AM12) tied for the lowest rank position in 2018 (Table 3.3). Similarly, there were seven individuals (AM2, AM3, AM5, AM7, AM8, AM9, and AM15) tied for rank position three in 2019 (Table 3.3). There was no significant variation in either normalized David's Scores (F=0.536, df=1, p=0.483) or resulting ranks (F=0.474, df=1, p=0.509) between 2018 and 2019. However, the difference in normalized David's Scores based on grooming *versus* aggressive interactions was significant in 2018 (F=7.772, df=1, p=0.021) but not in 2019 (F=0.138, df=1, p=0.719).

TABLE 3.3. Aggression-Based David's Scores Analysis Results for 2018 and 2019

ID	2018 David's Score	2018 Rank	2018 Categorical Rank	2019 David's Score	2019 Rank	2019 Categorical Rank
AM2	0.67	2	High	0.50	3	Middle
AM3	0.33	3	Middle	0.50	3	Middle
AM5	0.00	4	Low	0.50	3	Middle
AM7	0.00	4	Low	0.50	3	Middle
AM8	1.00	1	High	0.50	3	Middle
AM9	0.33	3	Middle	0.50	3	Middle
AM10	0.33	3	Middle	0.33	4	Low
AM12	0.00	4	Low	1.00	1	High
AM13	0.33	3	Middle	0.67	2	High
AM14	0.33	3	Middle	0.00	5	Low
AM15	0.33	3	Middle	0.50	3	Middle

There was no significant variation between the categorical ranks assigned in 2018 for either the grooming-based hierarchy and the priority-of-access hierarchy (F=4.859, df=1, p=0.055) or for the aggression-based hierarchy and the priority-of-access hierarchy (F=0.225, df=1, p=0.647). However, there was significant variation between the grooming-based and priority-of-access hierarchies for 2019 (F=5.657, df=1, p=0.0413). Finally, there was significant variation in ranks by the priority-of-access hierarchy between 2018 and 2019 (F=13.67, df=1, p=0.00494) (Table 3.4).

TABLE 3.4. Priority-of-Access to High Value Enrichment Categorical Ranking for 2018 and 2019

ID	2018 Categorical Rank	2019 Categorical Rank
AM2	High	High
AM3	High	High
AM5	High	Middle
AM7	Middle	Middle
AM8	Middle	High
AM9	Middle	Middle
AM10	Middle	Middle
AM12	Low	Low
AM13	Low	Middle
AM14	Low	Low
AM15	Low	Low

At the individual level, there was no significant variation from 2018 to 2019 in individual measures of either betweenness (F=1.29, df=10, p=0.3478) or closeness (F=0.90, df=10, p=0.5636). Overall measures of betweenness had no significant variation with either year (F=1.47, df=1, p=0.2425) or rank (F=0.81, df=2, p=0.4639). There was no significant variation in individual measures of closeness between 2018 and 2019 (F= 0.68, df=1, p=0.421) (Tables 3.5 and 3.6). However, there was a significant variation with closeness measures and rank (F= 6.36, df=2, p=0.009) and a significant interaction between rank and year (F=6.85, df=2, p=0.0071). Correlation results revealed a significant positive correlation between closeness and rank (r=0.46335, N=22, p=0.0299).

TABLE 3.5. Individual Sociality Measures Across 2018

Individual	Degree	Closeness	Betweenness	Eigen Value	Subgraph
AM2	6	0.0244	6.83	1.00	13.9
AM3	3	0.0217	0.00	0.662	8.03
AM5	0	0.00909	0.00	0.00	1.00
AM7	4	0.0227	1.17	0.820	10.7
AM8	6	0.0244	7.25	0.944	12.9
AM9	0	0.00909	0.00	0.00	1.00
AM10	2	0.0217	0.00	0.383	3.62
AM12	0	0.00909	0.00	0.00	1.00
AM13	2	0.0222	0.00	0.488	4.30
AM14	2	0.0222	0.00	0.488	4.30
AM15	3	0.0222	0.75	0.584	6.00

TABLE 3.6. Individual Sociality Measures Across 2019

Individual	Degree	Closeness	Betweenness	Eigen Value	Subgraph
AM2	4	0.0588	1.87	0.517	20.7
AM3	6	0.0625	2.98	0.742	40.2
AM5	2	0.0435	0.00	0.245	6.02
AM7	8	0.0667	11.4	0.855	52.9
AM8	9	0.0714	15.1	1.00	71.0
AM9	4	0.0588	1.98	0.510	19.7
AM10	5	0.0625	7.64	0.426	15.7
AM12	2	0.0417	0.00	0.160	4.29
AM13	4	0.0556	3.44	0.464	18.4
AM14	4	0.0476	0.00	0.626	29.7
AM15	2	0.0526	0.561	0.230	5.37

Further correlation analyses separating data by year revealed that, in 2018, closeness and rank were significantly positively correlated such that lower ranked individuals had higher closeness (r=0.68659, N=11, p=0.0196) (Fig. 3.1). However, in 2019 closeness and rank were significantly negatively correlated such that higher ranked individuals had higher closeness values (r= -0.58594, N=11, p=0.0582) (Fig. 3.2).

Figure 3.1. 2018 Adult Male Social Network

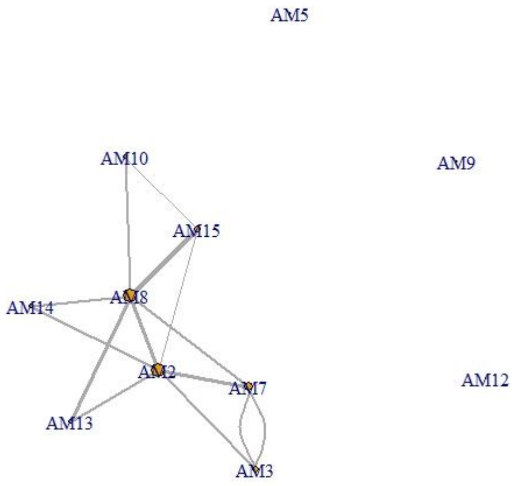
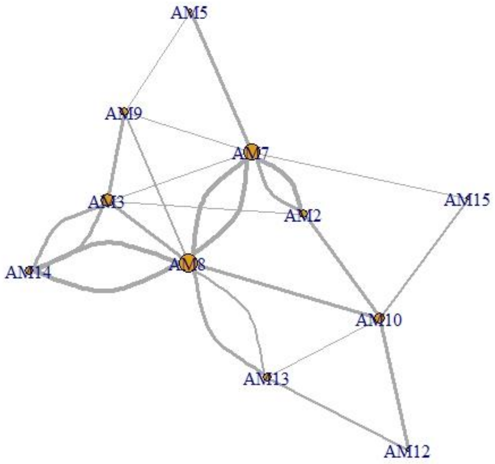


Figure 3.2 2019 Adult Male Social Network



III.IV. Discussion

David's Score analyses, particularly those based on aggressive matrices, have been frequently upheld as the standard for assessing linear dominance (Gammell et al., 2003). However, even in species known to form dominance hierarchies such as Japanese macaques, aggression-based analyses can be inadequate for assessing rank relationships among individuals. The variation displayed between the three calculated hierarchies demonstrates the highly complex nature of dominance. While aggression is the classic means of interpreting dominance, environmental factors of captive management such as provisioning, lack of predation, and more even sex-ratios may impact the expression of dominance and the degree and type of male-male interactions (De Waal, 1986; Ostner & Schülke, 2014b). What we see demonstrated in this group is that dominance must be assessed from a multi-directional approach which incorporates multiple benefits of high rank such as asymmetrical aggression, asymmetrical grooming receipt, and monopolization of preferred enrichment. While this model has been highly successful in management of despotic rhesus macaques (Adams, Majolo, et al., 2015; Capitanio, 1999; Westergaard et al., 1999), the interspecific variation between tolerance and despotism observed in Japanese macaques necessitates a more flexible and comprehensive approach to social dominance (Balasubramaniam et al., 2012; Chaffin, 1995; Lunardini, 1989). For example, AM3 was identified by long-term care staff as the most dominance male. However, according to our analyses AM3 only behaviorally ranked high based on grooming (Table 2) and priority-of-access (Table 4) models. As such, it may be important to assess dominance more fluidly, as context may dictate the expression of dominance behaviors and variation in which individuals express these behaviors.

It is also important to model shifts in behavior which may indicate changes in dominance relationships over time. AM8 was identified by care staff as the second ranking male in 2019, but not in 2018. In our analyses, AM8 displays high rank based on grooming in both 2018 and 2019, high rank based on aggression in 2018 but *not* 2019, and middle rank on priority-of-access in 2018 but high rank in 2019. This decrease in aggression-based rank between 2018 and 2019, when paired with the similar middle ranking of AM3 according to aggression, may be a function of established and secured position. It is possible that AM8 exerted more aggressive effort in 2018 which then tapered off upon attaining high rank in 2019. Further investigation of the grooming-based hierarchy variation between 2018 and 2019 revealed that while higher ranking males maintained stable levels of grooming behaviors, lower-ranking males increased their grooming efforts directed at higher-ranking males between 2018 and 2019. Shifts in dominance can happen rapidly and thus necessitate careful monitoring (Anderson, 2016; Takahashi, 2002).

These individual trends are further reflected in social network analyses. Individuals did not vary significantly in their betweenness or closeness measures across years (Table 6 and Table 7). This suggests that these social trends may be more consistent behavioral patterns akin to personality traits. Although there was a rank-closeness correlation in both 2018 and 2019, the flipped directionality of this correlation between years indicates that it was an individual-driven rank effect rather than a true rank-effect. As individuals increase rank over time, the centrality measures characterized within a rank class vary as well. As such, we are finding that individuals are driving changes in rank effects in centrality trends.

This suggests that individuals determine the nature of a group. If the highest rank class of individuals also have low centrality measures, this may contribute to a less socially stable and connected network within the social group. In terms of management, it is critical that care staff understand individual behavior and individual sociality as a crucial tool for social group maintenance and moderation. For example, if a middle-ranking male exhibits high levels of centrality (such as AM7), it would be beneficial for care staff to manage the group in such a way as to either maintain the rank of this individual or increase their rank which may increase group affiliation and cohesiveness.

Similarly, network maps such as Figures 3.1 and 3.2 in partnership with centrality measures *and* dominance assessment provide guidance for the formation of new groups. For example, removing an individual such as AM8 who is both dominant and highly central to the male network may have a destabilizing effect on male social relationships which could influence instability within the larger social group. However, other individuals of varying rank (AM5, AM12, or AM15) may be removed to form new one-male units without risking major shifts in the existing network and social trend towards cohesiveness. Ultimately, the use of species-specific models and individually-based centrality and dominance assessment would significantly improve the nuanced management, maintenance, and formation of large multi-male social groups.

III.V. Bridge to Chapter IV

The objective of Chapter III was to investigate how dominance rank in adult male Japanese macaques varies depending on the metric used in assessment. A secondary objective of this chapter was to examine how dominance rank assessments, when paired with social networking analysis, can be used to make management decisions for social groups under human care. The results presented here demonstrated that rank can be very contextual, with individual rank significantly varying dependent on whether one relies on a win-loss matrix composed of aggressive or affiliative interactions. A categorical approach may be more effective in broadly capturing how an individual functions within a group. Furthermore, dominance does not necessarily correlate to network centrality, meaning that removing a seemingly unnecessary middle-ranking individual can have highly destabilizing impacts for group cohesion. As such, Chapter III establishes a preferred metric for assessing dominance (categorical) and introduces a comparative dichotomy of aggressive *versus* affiliative behavioral patterning, which are necessary for the investigation of behavioral strategies and their efficacy as presented in Chapter IV. The study presented in Chapter IV will take an evolutionary approach to examining the success of aggressive *versus* affiliative social strategies in securing both dominance rank and fitness benefits.

CHAPTER IV

DOMINANCE, FEMALE CHOICE, AND REPRODUCTIVE SUCCESS IN ADULT MALE JAPANESE MACAQUES (*MACACA FUSCATA*)

This chapter includes previously unpublished material which is currently under review for publication with the American Journal of Primatology. *Material is reproduced with permission from Gartland, K.N., Biggs, N., Shreeve, C.M., and White, F.J. The author, Kylen N. Gartland, was the principle investigator for this work and is responsible for designing the study, behavioral data collection, statistical analyses, and manuscript preparation. Frances J. White is the graduate advisor for this dissertation and participated in study design, statistical analysis, and manuscript review. Nichole Biggs and Caitlin M. Shreeve are undergraduate research assistants who participated in data collection, statistical analyses, and manuscript preparation.*

IV.I Introduction

Life History Theory predicts that an individual's behavioral strategies reflect the changing costs and benefits of actions during their lifetime (Brommer, 2000; Buss, 2009; Del Giudice et al., 2016; Nettle & Frankenhuis, 2020; Wolf et al., 2007). Effort which is allocated to solving one adaptive problem often cannot be allocated to solving other adaptive problems; this creates a system of optimal trade-offs between allocations which will differ depending on variables such as individual qualities, life expectancy, and an individual's total energy budget. These varying behavioral strategies have differential impacts on an individual's reproductive success (Brommer, 2000). Individuals with a short expected life span engage in steeper future discounting, shifting to a strategy of immediate resource expenditure, risk taking, and intense competition (Buss, 2009). This can result in selection for species-typical psychological mechanisms that are flexible and respond to changes in environmental or cultural conditions (Lane et al., 2010; Nettle & Frankenhuis, 2020). For example, a single individual may become more risk-taking during times of famine. Likewise, an individual may display significantly different behavioral strategies in response to socioecological shifts such as changes in dominance rank or the adoption of age-related social roles (Weiss & King, 2015).

Behavioral strategies are an important component of sociality which broadly encompasses elements of social organization, the prevalence and type of social bonding, and the presence and intensity of hierarchical structure (Clutton-Brock & Harvey, 1977; Clutton-Brock & Janson, 2012; Kappeler, 2019; Kappeler & van Schaik, 2002). Sociality reflects an individual's position within the larger social unit and their patterns of engaging in both affiliative and aggressive behaviors with other group members. One of the most important guiding variables of sociality is an individual's dominance rank. Dominance is complex and can have variable impacts on outcomes such as reproductive success depending on both context and sex (Cowlishaw, 1991; de Ruiter, 1993; De Waal, 1986; Flack & de Waal, 2004; King et al., 2008; Rosenbaum et al., 2015; Snyder-Mackler et al., 2015; Sterck et al., 1997; Tsuji & Takatsuki, 2012; Van Doorn et al., 2002; Watts, 2010; Wolfe, 1984).

Dominance relationships and structures are more than dyadic interactions and can extend to include multiple social groups or multiple genetic lineages (Hinde, 1976). Classically, dominance is thought of as selecting for varying degrees of both fighting ability (and related traits such as physical size and strength) as well as social skills which grant individuals differential access to resources, particularly reproductive resources such as fertile females (Alberts et al., 2003; Bernstein, 1976, 1978, 1980, 1981; Coleman et al., 2011; Cowlishaw, 1991; de Ruiter, 1993; Majolo et al., 2012; Watts, 2010). Models of dominance weighted more heavily towards fighting ability often show an inverse U-shaped relationship between age and rank, with male condition decreasing as individuals move from prime adulthood into agedness (Watts, 2010) while models weighted more heavily towards social skills emphasize the role of the dominant male as buffering the social group against disruption or disturbance from any number of sources (Bernstein, 1976, 1978, 1980, 1981). This perspective emphasizes the importance of the protective function of the dominant male over the individual acquisition and monopolization of resources. Under this model, the observed increased genetic fitness in alpha males is dependent on the social skills necessary to maintain a society (Bernstein, 1976).

A critical aspect of dominance, either weighted towards fighting ability or towards social skills, is the policing function fulfilled by the dominant individual or individuals. Policing, which is defined broadly as the intervention by a third party in ongoing contests, has potentially costly risks to the intervening party (Flack, de Waal, et al., 2005). Studies of policing have found that it is an effective means of reducing the intensity of conflict (or terminating it entirely) when the most dominant individual is the intervening third party and, furthermore, that powerful policers are essential for maintaining social order and stability (Beisner et al., 2016; Beisner & McCowan, 2013; Flack et al., 2006; Flack, de Waal, et al., 2005; Flack, Krakauer, et al., 2005). Very broadly, it has been said that “a well-recognized hierarchy promotes social bonds and reduces violence" (De Waal, 1986). This reduction of violence through mechanisms such as policing can help reduce the costs of aggression, particularly the risk of injury (Watts, 2010). Therefore, while the presence of multiple males necessitates a biological system which selects for attributes such as size and fighting ability which enable a male to attain high rank, the dominant individual is also responsible for, and thus must be able to fulfill, a particular social role as well. Thus, a true conceptual understanding of the operation of dominance must look beyond the strictly agonistic aspects of attaining and maintaining dominance rank and incorporate measures of social skill such as affiliation (Bernstein, 1981).

With dominance rank granting an individual greater access to key limiting biological resources, individuals within a group may employ a variety of behavioral strategies in order to attain or maintain their rank. While most often these strategies are investigated from the perspective of aggression, both in terms of frequency and directionality, other experts suggest that affiliation must be equally considered when assessing behavioral strategies (Sussman et al., 2005). Affiliative behaviors are significantly more common than aggressive behaviors across all primate species, though the form and frequency of these behaviors vary across species, sex, social context, and individual (Cheney et al., 1986; Furuichi, 1983; King et al., 2008; Ostner & Schülke, 2014b; Smuts, 1985; Sussman et al., 2005). Social bonds between males, maintained by affiliative exchanges, can be crucial in the formation of coalitions and can have significant impacts on reproductive success (Berghänel et al., 2011; Gilby et al., 2013; Kawazoe, 2016; Kawazoe & Sosa, 2019; Ostner & Schülke, 2014b; Schülke et al., 2010; J. B. Silk, 1994; van Hooff & van Schaik, 1994; Young et al., 2014). Males may direct affiliation towards higher-ranking males in the hopes of future agonistic support and, furthermore, affiliative relationships between males may be dependent on sex ratios as groups with ratios closer to parity display higher rates of male-male affiliative behavior (Chapais et al., 1995; Hill, 1994).

One study estimated that group-living primates spend less than 10% of their activity budget in social behaviors, with less than 1% of this activity being agonistic or aggressive in nature (Sussman et al., 2005). As such, a focus solely on aggression and aggressive behavioral strategies can be an incomplete methodology for investigating the complex methods by which individuals may seek to (a) maintain or improve their position relative to a social group and (b) attain reproductive opportunities. Furthermore, incorporating both affiliative and aggressive behavioral strategies are necessary to account for species and population-specific factors which may constrain the pursuit of the previously mentioned goals and evaluate the specific form that varying behavioral strategies may take.

Dominance, and its balance with prosocial behavior, become particularly complex within the context of despotic systems like those found in Japanese macaques (*Macaca fuscata*). Japanese macaques form multi-male multi-female social groups of approximately 40.8 ± 28.95 individuals (Fooden & Aimi, 2005; Itani et al., 1963). Similarly to other macaques, *M. fuscata* create matrilineal, female-bonded groups in which females remain in their natal groups while males over 5 years of age disperse and join new groups (Fooden & Aimi, 2005; Itani et al., 1963; Sprague et al., 1998; Takahashi, 2002). While male Japanese macaques may display sexual behaviors while still juveniles, the testes do not descend into the scrotum until approximately 4.5 years of age (Fooden & Aimi, 2005; Soltis et al., 2001; Takahata et al., 2005). Despite reaching physical sexual maturity, and emigrating from the natal group, at approximately 5 years of age, adult males are not fully socio-sexually mature until at least 8.5 years of age. However, this may be accelerated by artificial provisioning.

Japanese macaques are classified as Grade 1 in dominance style and form highly despotic male and female hierarchies (Chaffin, 1995; Eaton, 1976; Matsumura, 1999; Suzuki et al., 1998; Takahashi, 2002; Watanabe, 2008; Zhang & Watanabe, 2014). As is typical of matrilineal species with female philopatry, female offspring inherit their rank from their mothers and matrilineal relations (Anderson, 2016; Takahata et al., 1998; Wolfe, 1984). For males, the acquisition of long-term high rank for an adult male may be impacted by any number of environmental or demographic factors including tenure of previously dominant males, social network structure, age of current resident males, etc. (Kawazoe & Sosa, 2019; Suzuki et al., 1998; Takahashi, 2002; Takahata et al., 2005).

In the discussion of dominance and reproduction, it is important to note a unique departure from the classic model in which dominant males have the greatest reproductive success (de Ruiter, 1993; Rodriguez-Llanes et al., 2009). While there is some evidence for the importance of dominance on the paternity of infants (Soltis et al., 2001), this positive correlation between reproductive success and rank has not been consistently observed in Japanese macaques, as reproductive success of dominants may be significantly influenced by competition with non-troop males, female estrous synchrony, operational sex ratio, and female choice (K. N. Gartland et al., 2020; Hayakawa, 2008; Hayawaka & Soltis, 2011; Inoue et al., 1993; Inoue & Takenaka, 2008; Kutsukake & Nunn, 2006; Soltis et al., 1997; Takahashi, 2001; Takahata et al., 2005).

Female choice may have particularly prevalent impacts (Hayakawa, 2008; M. A. Huffman, 1987; Inoue & Takenaka, 2008; Soltis et al., 1997). One study showed that a majority of offspring were fathered by low-ranked males rather than high-ranking males (Inoue & Takenaka, 2008). Furthermore, females may enact some degree of influence by mating with high-ranking males after conception and avoiding less “attractive” males during their ovulatory periods (Inoue et al., 1993; Soltis et al., 1997). Attractive males have been variably identified as those with whom females preferentially interact as measured by either affiliative encounters, proximity, or female maintenance of consortship (Perloe, 1992; Soltis et al., 1997). While both high-ranking males and lower-ranking, but more attractive, males may both experience quantifiable mating success – this does not necessarily translate to reproductive success (Soltis et al., 1997). The effects of choice can be further increased when females experience estrous synchrony which inhibits the ability of high-ranking males to monopolize fertile females and exert control over mating access (Kutsukake & Nunn, 2006; Matsubara, 2003; Ostner et al., 2008; Schülke & Ostner, 2008). This frequently-observed disparity between rank, copulation frequency, and reproductive success suggests the existence of alternative mating strategies such as sneak-mating, extra-troop mating, or appealing to female choice which is utilized by lower-ranking males (Inoue & Takenaka, 2008; Otani et al., 2020; Soltis et al., 1997; Takahata, Huffman, Suzuki, Koyama, & Yamagiwa, 1999).

IV.I.I. Hypotheses and Predictions

The population of Japanese macaques in residence at the Oregon National Primate Research Center provide an unusual opportunity for examining the interplay between dominance rank, female choice, and reproductive success. Unlike wild populations, the ONPRC population has no access to extra-troop individuals. As such, there is no risk to dominant males of mating interference from non-troop males. This population offers an opportunity to examine the operation of dominance rank *versus* female choice on male reproductive success.

In this study, we examine variation in behavioral strategies across adult males in a semi free-ranging group and the success of these strategies as measured by male rank and male reproductive success. Based on the previously reviewed literature we propose to construct and compare two models: one representative of a dominance-based reproductive strategy and the second representative of a female choice-based reproductive strategy. Based on the previously-reviewed importance of policing, coalitionary support, and fighting ability in attaining dominance rank, the dominance model will be based on aggressive behavior and affiliation with other males. From the reviewed literature on female choice, the second model will be based on affiliation with female partners. We hypothesize that if dominance is the primary driver of reproductive success, then more aggressive males should both hold higher rank and have higher reproductive success. If female choice is the primary driver within this population, then affiliative males should have higher reproductive success without necessarily holding higher dominance rank.

IV.II Methods

IV.II.I Study Subjects and Age Classifications

At the start of the study, the group included 156 females and 109 males aged between 0-25 years. The ONPRC provided age classification for the group (K. Coleman, pers. comm.). The provided age classifications were as follows: infants (<1 year), juveniles (>1 year to 4 years), subadults (>4 to 7 years), adults (>7 to 15 years) and aged (>15 years). As part of general practices at the ONPRC, animals were given unique dye markings on their backs, heads, arms, shoulders, and/or rumps. These allow for individual identification of all members of the group from the observation tower.

Juveniles are visually distinguished from infants by their given markings, and also by behavioral cues such as their decrease in nursing and increase of independence for their mother at one to two years of age (Coleman, Robertson, and Bethea 2011; personal observations). Furthermore, juveniles of approximately one year of age born in extra-troop harem groups had been introduced into the group. These individuals were identified by black dye on the top of their heads. For this study, we focused on 17 males classified as aged or adult individuals.

IV.II.II Behavioral Observations

We conducted observations in two distinct periods: June to September 2018 and July to September 2019. Observers took data Monday through Friday from approximately 0900 to 1600 h. Both data collection periods overlapped with the birth season, which ranges from May-August for Japanese macaques at the ONPRC. Most births typically occur in June and July (Coleman et al., 2011). We collected 512 hrs of data with approximately equal effort per male per study period (Table 4.1). However, from the first period of data collection three males died and one male was removed and placed in a harem. In the second period of data collection one male aged into an adult and was added to the study. The subjects are frequently observed both by care staff and visitors and thus are habituated to human presence.

Table 4.1. Study subjects, age classifications, rank, and hours of observation

Focal	Rank	Age 2018 (years)	Age-Class 2018	Data Hours 2018	Data Hours 2019	Total Hours
AM1	High	25	Aged	11	*Deceased*	11
AM2	High	21	Aged	11	25.75	36.75
AM3	High	20	Aged	11	25.5	36.5
AM4	High	18	Aged	11	*Deceased*	11
AM5	High	17	Aged	11	26	37
AM6	Low	9	Adult	11	*Removed*	11
AM7	Middle	10	Adult	11	26	37
AM8	High	8	Adult	11	26	37
AM9	Middle	8	Adult	11	25.75	36.75
AM10	High	8	Adult	11	25	36
AM11	Middle	8	Adult	11	*Removed*	11
AM12	Low	9	Adult	11	25.5	36.5
AM13	Low	8	Adult	11	26	37
AM14	Low	7	Adult	11	25.75	36.75
AM15	Middle	7	Adult	11	25.75	36.75
AM16	Low	6	Sub-Adult	*Immature*	25.5	25.5
AM17	Low	6	Sub-Adult	*Immature*	26.5	26.5

We conducted fifteen minute focal follows of single individuals using one-minute instantaneous scans following established methodology (Altmann, 1974). Approximately 15 focal follows were collected per day with breaks in observation between follows (1-2 follows per subject per day). The order of focal follows was randomly selected so each individual was the subject of at least 1 follow per day at different times of the day.

We recorded solitary, agonistic, socio-sexual, and social behaviors. Types of social interactions such as agonism and socio-sexual interactions were given their own category to allow a more comprehensive set of specific behaviors. We recorded directionality of all social behaviors. Partner classifications were identified in all social, agonistic, and socio-sexual behaviors when possible. If individual identification of social partners was not possible, then social partner was classified by sex and age-class. These classifications included adult female, subadult male, juvenile (with sex if possible to determine), infant, and unknown. Furthermore, when possible we recorded if a male was interacting with a natal or non-natal juvenile.

IV.II.III. Data Analysis

In order to examine individual strategies, we first divided social behavior into two categories – affiliation and aggression. We calculated behavioral rates of each mutually-exclusive aggressive or affiliative behavior for each of the 17 males from frequency per observation hours. We then used these behavioral rates to construct the female choice and dominance models. The female choice model included grooming with females (separated by directionality), non-grooming affiliative behaviors with females (separated by directionality), initiated affiliative interactions, and terminated affiliative interactions. The aggressive profile included aggression (separated by directionality and sex of adult partner), affiliation with adult males, initiated aggressive interactions, and terminated aggressive interactions. We separated behaviors by directionality of behaviors, sex-class of social partner, and initiation/termination of behaviors where appropriate to capture subtler nuances of social decision-making.

In order to identify similarity between males in their social patterning, we used principal components analysis (PCA) to cluster individuals according to similarity in their separate dominance and female-choice profiles. As all variables were non-overlapping, we did not run tests to determine inclusion or exclusion criteria. In order to identify statistically significant clusters, we used the nonparametric MODECLUS procedure within SAS ©, 9.4.1 (Cary, NC, USA) following methodology established in previous studies (Gebhardt-Henrich et al., 2014; Hernández et al., 2007; McLaughlin et al., 1999; Reeves & Richards, 2009; St.-Laurent et al., 2000). The particular advantages of MODECLUS over other clustering methods lies in its lack of assumption of distribution of the variables and the lack of bias towards uniformity in cluster size, shape, variance, or dispersion. An in-depth description of the advantages of MODECLUS *versus* other statistical methods is presented in Stl-Laurent *et al*. 2000. The MODECLUS procedure is used to statistically examine density estimates, cluster membership and the number of resultant clusters at different significance levels. We used method 1 for all MODECLUS procedures. We used the density parameter (R-value) in order to identify four to five clusters including single-member clusters for the aggressive and affiliative profiles.

After establishing the number and membership of profile clusters (hereafter referred to as strategy clusters), we then ran one-way ANOVAs to examine variation between the clusters in: 1) dominance rank and 2) reproductive success at age eight years. We ran these ANOVAs for both the female-choice strategy clusters and the dominance strategy clusters to examine which, if either, emerged as a potential driving factor in rank attainment or reproductive success.

Categorical dominance rank based upon a priority-of-access model for individuals within this population had been previously established and kept updated (K. N. Gartland et al., 2020). Males were ranked as either High (1), Middle (2), or Low (3)

(Table 4.1). Some individuals experienced fluctuations in status within and without their assigned categorical rank throughout the study period. In order to address this, we conducted analyses based on the categorical rank that the male held for the majority of their observation hours.

Data pertaining to reproductive success were obtained through routine genetic testing done by the ONPRC. Through these genetic data, we were able to establish the total number of offspring for each male as well as the male's age when each offspring was sired. Reports from the ONPRC, which were supported by the supplied genetic data, indicate that adult males within this population often reach peak reproductive success from ages seven to nine. Additionally, due to interruptions of routine genetic analysis caused by COVID-19, updated paternity data were unavailable for four subjects (AM14, AM15, AM16, and AM17). Because of these complications and due to the wide age-spread of study subjects, we chose to subset the total reproductive success into the number of offspring each male had sired by age eight in order to include the maximum number of males in reproductive success analyses. Number of sired offspring ranged from 2 to 11 (Table 4.2).

Finally, we ran a Pearson's correlation of the reproductive data against male scores on the first principle component of both the dominance and female choice PCA outputs. All analyses were conducted using SAS 9.4.1.

Table 4.2. Individual Reproductive Success by Age Eight

Individual	# of Offspring
AM1	2
AM2	0
AM3	1
AM4	1
AM5	0
AM6	2
AM7	6
AM8	11
AM9	5
AM10	4
AM11	2
AM12	10
AM13	2
AM14	*No data*
AM15	*No data*
AM16	*No data*
AM17	*No data*

IV.III. Results

The PCA for female choice profiles indicated that approximately 98.10% of variance was explained within the first five principle components (eigenvalues: PC1: 2.89, PC2: 1.88, PC3: 1.01, PC4: 0.74, PC5: 0.34). The proportion of variance explained by each individual component ranged between 4.87% and 41.23%. The PCA for dominance profiles indicated that approximately 91.89% of variance was explained within the first five principle components (eigenvalues: PC1: 3.30, PC2: 2.72, PC3: 1.29, PC4: 1.05, PC5: 0.83). The proportion of variance explained by each individual component ranged between 8.30% and 32.97%.

Using a standard of ±0.4 for significant loading (Brent et al., 2014), we found that PC1 for the dominance profile was characterized by increased aggression given to adult females (+0.49), aggression given to adult males (+0.40), aggression initiated (+0.52), and affiliation received from adult males (+0.44). PC2 for the dominance profile was characterized by increased aggression received from juveniles and subadults (+0.54), aggression received from adult females (+0.42), and aggression received from adult males (+0.56). As such, we characterized individuals or dominance profile clusters according to how they fell on the axis created by PC1 and PC2 with high scores on PC1 representing high aggression and high scores on PC2 representing submissiveness/low aggression.

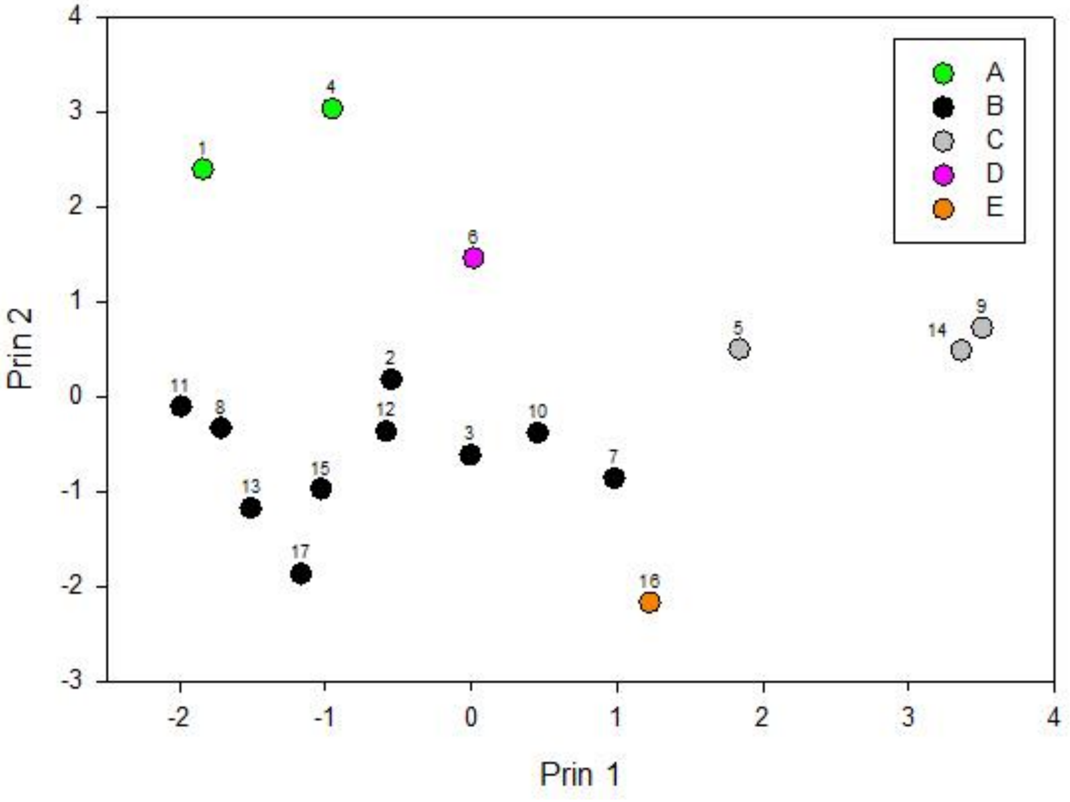
PC1 for the female choice profile was characterized by increased affiliation received from adult females (+0.40), affiliation given to adult females (+0.51), affiliation initiated (+0.49), and affiliation terminated (+0.46). PC2 was characterized by increased mutual affiliation (+0.52) and bi-directional grooming (+0.46). As both PC1 and PC2 measured for high affiliation, low scores on either axis were taken as representative of a less affiliative strategy.

The MODECLUS procedure run at R=0.90 resulted in five female choice behavioral clusters, including two single-member clusters (Table 4.3) (Figure 1).

Table 4.3. Cluster Statistics from MODECLUS Procedure on Affiliation Profiles

Cluster	Frequency	Maximum Estimated Density	Boundary Frequency	Estimated Saddle Density
A	2	0.04623237	0	.
B	10	0.18492949	0	.
C	3	0.06934856	0	.
D	1	0.02311619	0	.
E	1	0.02311619	0	.

Figure 4.1 Plot of Male Clusters According to the First Two Principal Components of Affiliative Profiles

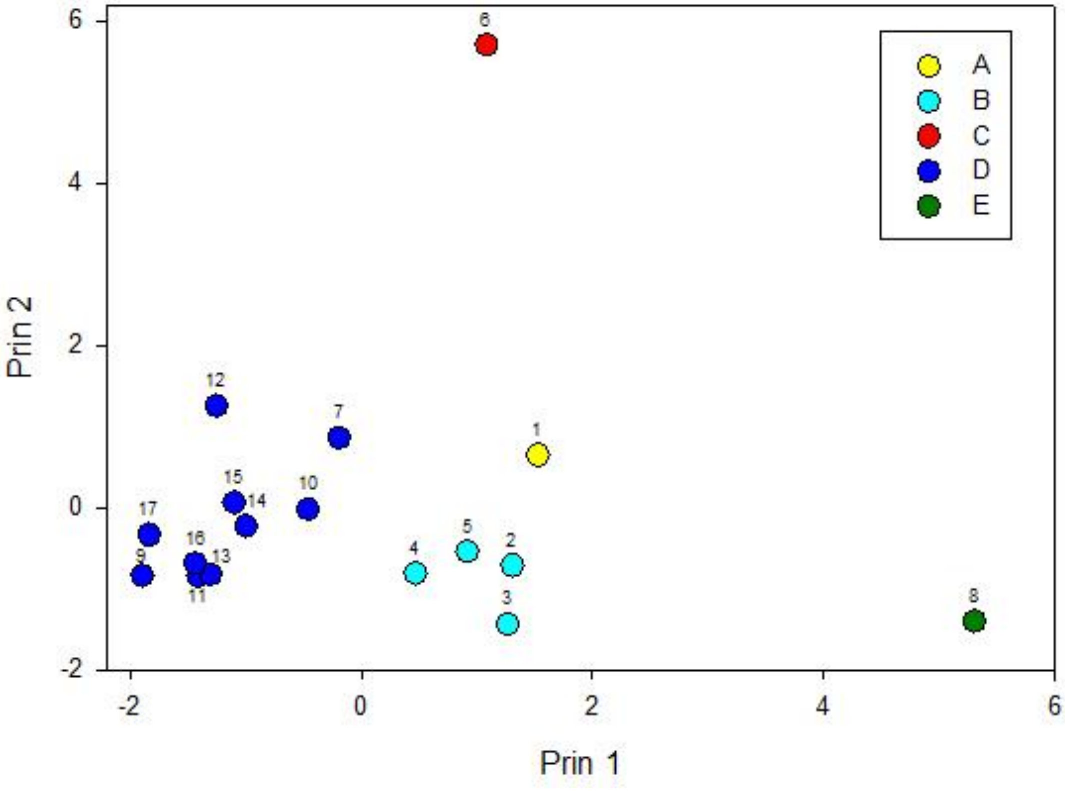


The MODECLUS procedure run at R=0.7 resulted in five dominance behavioral clusters, including three single-member clusters (Table 4.4) (Figure 4.2).

Table 4.4. Cluster Statistics from MODECLUS Procedure on Aggression Profiles

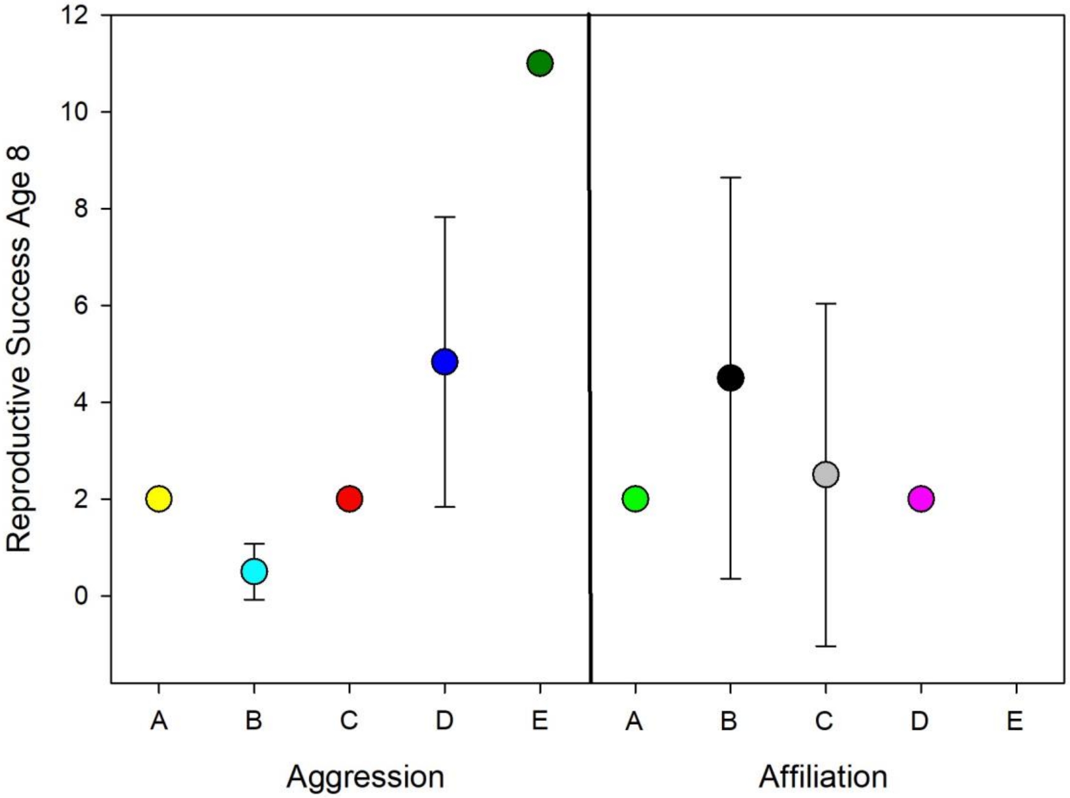
Cluster	Frequency	Maximum Estimated Density	Boundary Frequency	Estimated Saddle Density
A	1	0.03821247	0	.
B	4	0.15284989	0	.
C	10	0.30569977	0	.
D	1	0.03821247	0	.
E	1	0.03821247	0	.

Figure 4.2. Plot of Male Clusters According to the First Two Principal Components of Aggressive Profile



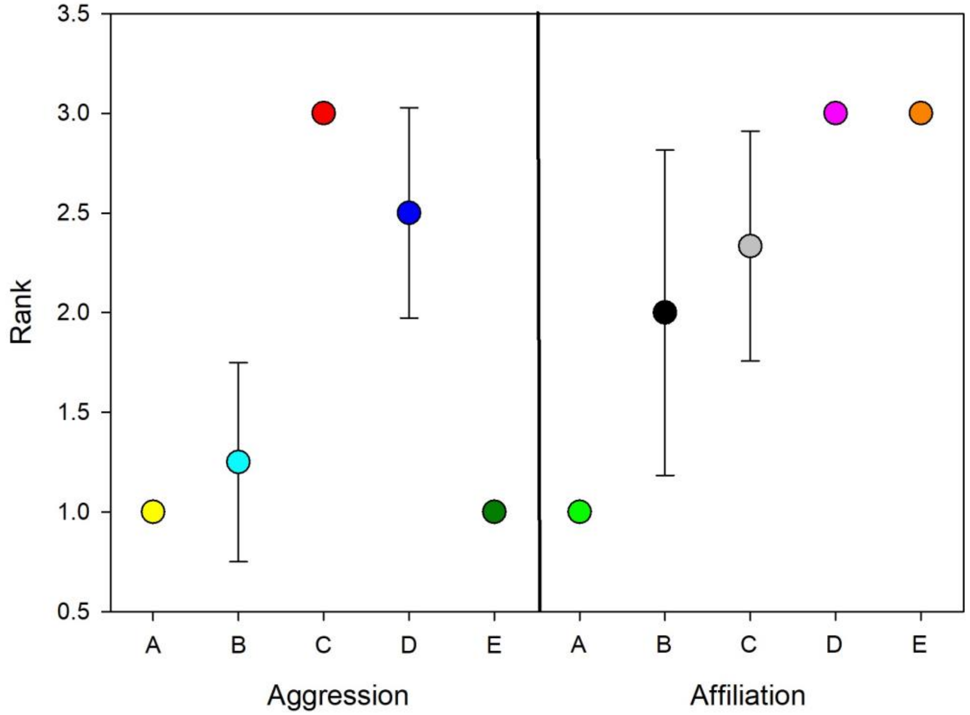
Results of the ANOVA examining variation in reproductive success between female choice profile clusters revealed no significant variation between clusters (F=1.77, df=3, p=0.17) (Figure 4.3a). However, there was significant variation in reproductive success between dominance profile clusters (F=19.92, df=4, p < 0.0001) (Figure 4.3b).

Figure 4.3 Reproductive Success According to (a) Affiliation Clusters and (b) Aggression Clusters



There was significant variation in categorical dominance rank both between female choice profile clusters (F=7.37, df=4, p=<0.01) (Figure 4.4a) and between dominance profile clusters (F=27.21, df=4, p < 0.0001) (Figure 4.4b).

Figure 4.4. Dominance Rank According to (a) Affiliation Clusters and (b) Aggression Clusters



Results of the Pearson's correlation were not significant for male reproductive success against their scores on the first principle component for both the female choice (r = -0.04, N=39, p=0.81) and dominance (r=0.20, N=39, p=0.4923) PCA outputs.

IV.IV Discussion

While the assumed evolutionary advantage of dominance is increased reproductive success (Chapais, 1983; de Ruiter, 1993; Majolo et al., 2012; Rodriguez-Llanes et al., 2009), the data has not supported this in all populations. In the case of

Japanese macaques, there is both evidence for a positive relationship between dominance and fitness in some populations (Inoue et al., 1990; Soltis et al., 2001) and for no significant relationship between dominance and fitness in others (Inoue et al., 1993; Takahashi, 2002; Takahata, Huffman, Suzuki, Koyama, & Yamigawa, 1999). Both non-troop male mating (Hayakawa, 2008; Sprague, 1991) and female choice (Huffman, 1992; Huffman, 1987; Inoue & Takenaka, 2008; Perloe, 1992; Soltis et al., 1997) may interrupt the efficacy of dominance as a mating strategy.

The population of Japanese macaques at the Oregon National Primate Research Center (ONPRC) offers a unique opportunity to compare and contrast dominance and female choice without the potentially confounding variable of non-troop males. We constructed two behavioral models representing a dominance mating strategy and a female choice mating strategy. The dominance model or profile took into account typical behaviors advantageous to males seeking to obtain and maintain high rank such as fighting ability, policing, and coalition formation which we assessed using measures of aggression and male-directed affiliation (Chapais, 1995; Eaton, 1974; Schülke et al., 2010; Van Doorn et al., 2002). The female choice model or profile was based on previously described “attractive” qualities in chosen males, namely measures of bi-directional affiliation with females (Soltis et al., 1997). Using these models, we were able to contrast two behavioral strategies: pursuit of dominance and pursuit of female favor.

Our results indicated that males tended to cluster across a spectrum of each strategic model. Males that clustered together based on high aggression, and thus high investment in a dominance strategy, were more successful in holding higher rank than males who were less aggressive (Fig. 2 & Fig. 4b). However, the less aggressive and less dominant males had significantly higher reproductive success than the more aggressive dominant males (Fig. 3b).

Based on these results, we expected to see significant variation in reproductive success between the female choice-based behavioral clusters. However, we found that a majority of males (N=10) employed similar affiliative strategies. There was no significant variation in reproductive success between the males that affiliated highly with females and those that did not (Fig. 3a). On comparison of males across dominance and female choice profile, we found that clustering in one profile did not necessarily predict clustering in the other. For example, a male clustering as highly aggressive and highly dominant did not necessarily cluster as less affiliative with females.

The significant variation in rank between the female choice clusters is likely an artefact of the two single-member clusters. The individuals in Cluster D and Cluster E are both low ranking, as opposed to the mix of rank membership in Clusters B and C and the high-ranking membership of Cluster A.

Our results indicate a potential new dimension of male attractiveness and female choice. Our results could potentially be interpreted in two ways. Firstly, it is possible that females select “attractive” males based on a combination of their affiliative *and* aggressive behavioral patterns. Females may reject a highly affiliative male if he is also highly aggressive while preferentially mating with highly affiliative males who engage in lower aggression.

Another alternative is that the males who are both highly affiliative and highly aggressive are engaging in competition with other males or unsuccessful mate-guarding attempts and these investments are lowering their actualized reproductive success. The potential fitness costs of mate-guarding and consortships, especially when female estrous synchrony is an active variable, have been previously demonstrated (Kutsukake & Nunn, 2006; Matsubara, 2003; Ostner et al., 2008; Otani et al., 2020).

Another study suggested that female Japanese macaques show particular preference for middle-ranking males over high-ranking males in a captive environment (Huffman, 1992). Personal communications from ONPRC staff report a pattern in which many offspring are routinely sired by the younger (eight and nine-year old) adult males rather than the older and more hierarchically-established males, potentially supporting a pattern in which females prefer the more middle-ranking males. However, when controlled for age at siring, we still found significant variation between individuals indicating that the benefits of this potential preference are not equally experienced across all individuals.

In summary, our results support female choice over dominance rank as a guiding factor in accounting for variable reproductive success among adult males. Despite a lack of threat from predators or non-troop males, dominant males still fail to routinely achieve high reproductive success. We suggest a longitudinal behavioral tracking of males as a potential next investigative step. If we can track male reproductive success through time with a specific aim to compare success as they behaviorally adapt to shifts in their social environment, we can potentially look at the variation in success individuals experience either across social status states or between behavioral strategies.

IV.V Bridge to Chapter V

The objective of Chapter IV was to examine how individuals engage in differential behavioral strategies and what impact these strategies have on their ability to gain high dominance rank and reproductive success. The results presented in this chapter demonstrate that while highly aggressive strategies are effective for gaining rank, less aggressive strategies were more effective for reproductive success. While most individuals employed similar affiliative strategies, affiliative trends did not predict aggressive trends (or vice versa). There is indication of alternative mating strategies within this population, as indicated by AM12. In sum, Chapter IV provides a structure from which to examine individual behavior while highlighting the importance of examining aggressive and affiliative behaviors independently rather than as subsumed under the broader umbrella of "social behavior". Chapter IV examines individual behavior from an independent perspective, while Chapter V will incorporate a broader group perspective of social behaviors. The study presented in Chapter V will use a biological markets framework to examine how an individual's demography impacts the degree to which they engage in affiliative and aggressive behaviors, who they engage with, and their positionality in the greater social network.

CHAPTER V

TRADING ON THE BIOLOGICAL MARKET: AN EXAMINATION OF DEMOGRAPHY, SOCIALITY, AND NETWORK CENTRALITY IN ADULT MALE JAPANESE MACAQUES (*MACACA FUSCATA*)

This chapter includes previously unpublished material which is currently under review for publication with Folia Primatologica. *Material is reproduced with permission from Gartland, K.N. and White, F.J. The author, Kylen N. Gartland, was the principle investigator for this work and is responsible for designing the study, behavioral data collection, statistical analyses, and manuscript preparation. Frances J. White is the graduate advisor for this dissertation and participated in study design, statistical analysis, and manuscript review.*

V.I. Introduction

Biological Market Theory has been used to understand how individuals or "traders" from different classes engage in interactions which function as exchanges of biological commodities such as key resources or social services (Noë & Hammerstein, 1994). Biological markets happen when 1) individuals can exert differential degrees of control over commodities, 2) there are multiple potential trading partners an individual may choose from, 3) there is competition between individuals to be selected as a trading partner, and 4) that the value of commodities is determined by supply and demand (Noë, 1992, 2017; Noë & Hammerstein, 1994). A major commodity or "currency" identified in primates is grooming, which has been observed being traded for reciprocal grooming, access to infants, support in agonistic conflicts, and mating access (Barrett & Henzi, 2006). In a biological market, an individual's affiliative interactions (particularly social grooming sessions) are commodities exchanged with a given social partner as the selected trading partner. Within the biological market, individuals may have different strategies. They may seek frequent affiliative interactions with numerous partners, or be more selective in the quality and quantity of trading interactions.

Individuals will vary in both the type and value of commodities available to them. An individual's ability to exert control over commodities can, in the context of non-human primates, be tied to dominance. Dominance rank has been demonstrated to allow individuals greater access to, or even monopolization of, key biological resources (Cowlishaw, 1991; de Ruiter, 1993; Majolo et al., 2012; Watts, 2010). We can, therefore, view dominance rank as granting an individual greater status within the biological market.

Dominance is a complex phenomenon that varies greatly between species and sexes. It can be related to physical condition and fighting ability, with dominance and age forming an inverse-U shaped relationship (Watts, 2010). A male's ability to retain high rank reaches a peak then decreases as he transitions from prime adulthood into agedness (Watts, 2010). However, dominance that is based on social skills is often reflected in high rates of social interactions, affiliation, and group centrality (Bernstein, 1978, 1980, 1981). When dominance selects for social skills, we do not expect rank to decline with age, thus allowing an individual to monopolize the biological market with affiliation as a prime commodity. In such cases sociality, as measured by network theory and behavioral trends, can be used to examine an individual's positionality within a biological market.

Social network theory seeks to compose networks of individuals or components (nodes) and their connections (ties) which can be utilized to understand the interplay between individuals, between individuals and the larger group, and between groups (Wey et al., 2008). Social network analysis traditionally employs a few key centrality measures which mathematically represent an individual's positionality within the network. These measures include degree, betweenness, closeness, and eigen value. Degree represents the total number of direct connections or number of independent partners that a focal individual interacted with (McCowan & Beisner, 2017; Wey et al., 2008). If an individual has, through dominance rank (attained via fighting ability or social skills) or otherwise, secured a highly central position within a network then we should also expect that individual to be a high value trading partner on the biological market.

Japanese macaques (*Macaca fuscata*) offer an intriguing challenge to this proposed Biological Market framework of dominance, age, sociality, and group centrality. Unlike other hierarchical species, Japanese macaques have been demonstrated to depart from the traditional inverse-U relationship between age and dominance. A population on Kinkazen Island, Japan showed a humped age-rank curve in which males aged 15-19 years monopolized high rank, but then decreased at or after 20 years of age (Takahashi, 2002). This study also found a relationship between rank and tenure whereby male rank tended to increase as their group tenure increased with the departure or disappearance of the high-ranking male acting as a necessary social mechanism for rank changes (Takahashi, 2002). This trend by which male rank and age are closely positively related has also been reported for semi free-ranging populations (Eaton, 1976; K. N. Gartland et al., 2020). It is important to note that Japanese macaques emigrate from their natal groups at around 5 years of age and from then on may have widely varying group tenures (Fooden & Aimi, 2005). Male group tenure has been reported to vary from 0.2 to 5.3 years on Kinkazan, 0.2 to 5.7 years on Arashiyama, and 1.0 to 9.5 years on Yakushima (Sprague et al., 1998). Full sociosexual maturity does not occur until at least 8.5 years for males, though can occur earlier in provisioned or semi free-ranging populations (Fooden & Aimi, 2005). Although some males in provisioned populations have been recorded as surviving until 20+ years of age, studies suggest that males greater than 20 years of age are no longer reproductively active due to age-related degeneration (Fooden & Aimi, 2005). However, males may begin showing signs of age-related health conditions, particularly kyphosis or curvature of the spine resulting in hunching and impaired movement, at age 15 years (Hamada & Yamamoto, 2010). However, if prime body condition is not a necessary attribute for dominance due to a decreased emphasis on fighting ability, Japanese macaque males may be able to maintain high rank despite physical infirmity particularly with extended group tenure.

V.I.I. Hypotheses

Based on this, we set out to investigate the relationship between demography (specifically dominance rank and age), sociality, and group centrality within adult males residing in the semi free-ranging group of Japanese macaques at the Oregon National Primate Research Center (ONPRC). Using Biological Market as a framework, we hypothesize that:

(1) Adult males who hold high rank also hold central positions within biological markets and can thus limit their exerted social energy. If this hypothesis is

supported, we predict that high-ranking males should (a) have higher rates of received affiliation than lower ranking males, (b) engage in more given aggression as they can provide more successful coalitionary support, (c) interact less with lower-ranking males because there is little value in this commodity to them, and (d) show a highly central position within the social network reflective of their centrality in the biological market.

(2) Younger adult males have less central positions within the biological market and must thus exert higher social effort to secure trading partners. If this hypothesis is supported, we predict that younger males should (a) have higher rates of given affiliation than older males, (b) have higher rates of affiliation across age and sex classes than older males, (c) interact more with other adult males as a means of establishing high value trading relationships, and (d) show peripheral positions within the social network.

V.II Methods

V.II.I Study Subjects and Location

This study was conducted on the Japanese macaques (Macaca fuscata) in residence at the Oregon National Primate Research Center (ONPRC) in Beaverton, Oregon, USA. This research population has been maintained in a semi free-ranging state since 1964. The group is housed in a 1-acre outdoor corral which is equipped with steel walls, two observation towers, and a number of structures for play and enrichment. In addition to the outdoor corral, the group also has constant access to an indoor feed room which measures approximately 3 by 12 meters. The group is fed a primary diet of commercial monkey chow which is supplemented by enrichment (grains, fruits, and vegetables) twice daily. Water is available ad libitum. The group is cared for on a daily basis by a team of animal care technicians and overseen by multiple management groups including the Behavioral Science Unit.

The group fluctuated in exact membership throughout the study but ranged in total from 221 to 245 individuals (Table 5.1). Age class assignments were provided by the ONPRC and modified only slightly. The original ONPRC classifications were as follows: infant (<4 yrs), subadult (>4-7 yrs), and adult (>7yrs) (K. Coleman, pers. comm.). For the purposes of our study, we subdivided the "infant" category into "infant" (<1 yrs) and "juvenile" (>1-4 yrs). In Japanese macaques, females reach sociosexual maturity at approximately 3.5-4yrs while males reach sociosexual maturity closer to 7 years (Fooden & Aimi, 2005). As such, we included the "subadult" category only for males.

Table 5.1. Group Composition in 2018 and 2019

	Infant	Juvenile Male	Juvenile Female	Subadult Male	Adult Male	Adult Female	Total
2018	5	62	70	8	16	60	221
2019	12	51	55	23	15	89	245

For this study, we collected data on all adult males within the population. Adult males ranged in age from 7 to 25 years (Table 5.2). The exact number of study subjects varied over the course of data collection. AM1 and AM4 died in October 2018 and were thus unavailable for the 2019 study period. AM6 and AM11 were removed from the main population to form new extra-troop harem units before the 2019 study period. Also

AM14, AM16, and AM17 were too young to be included in data collection in 2018, but aged into the study in 2019.

Table 5.2. Study subjects, age, age class, and rank across 2018 and 2019.

	2018			**2019**		
	Age	**Age Class**	**Rank**	**Age**	**Age Class**	**Rank**
AM1	25	Aged	High		*Deceased*	
AM2	21	Aged	High	22	Aged	High
AM3	20	Aged	High	21	Aged	High
AM4	18	Aged	High		*Deceased*	
AM5	17	Aged	High	18	Aged	High
AM6	9	Adult	Low		*Removed*	
AM7	10	Adult	Middle	11	Adult	Middle
AM8	8	Adult	Middle	9	Adult	High
AM9	8	Adult	Middle	9	Adult	Middle
AM10	8	Adult	Middle	9	Adult	Middle
AM11	8	Adult	Low		*Removed*	
AM12	9	Adult	Low	10	Adult	Low
AM13	8	Adult	Low	9	Adult	Middle
AM14	6	*Subadult*		7	Adult	Low
AM15	7	Adult	Low	8	Adult	Low
AM16	6	*Subadult*		7	Adult	Low
AM17	6	*Subadult*		7	Adult	Low

V.II.II Data Collection

Data were collected in two distinct study periods. The first study period spanned from June to September 2018 and the second from July to November 2019. During these periods, observers collected behavioral data at the ONPRC from approximately 08:30 to 16:00 Mondays through Fridays.

We conducted 15-minute focal follows with 1-minute instantaneous scans following previously established methodology (Altmann, 1974; Gartland et al., 2020). Study subjects were individually-identifiable by a combination of dye-markings on their backs and limbs (placed bi-annually by ONPRC management on all members of the population), and distinctive facial or pelage markings. Focal follows were conducted from the two observation towers overlooking the Japanese macaque habitat. A total of three observers collected data including K.N.G. (2018 and 2019), C.M.S. (2019) and N.B. (2019). Interobserver reliability was established with a minimum of 85% consistency in July of 2019 before beginning data collection and was re-tested in August and September 2019. Each observer had a randomized focal follow list, such that each observer conducted a focal follow on every study subject at least once per day and there was no overlap of follows between observers (i.e. no two observers were ever observing the same focal individual at the same time).

Behavioral collection included recording an array of social and solitary behaviors (Supplementary A). Due to the study's focus on sociality, social behaviors were subdivided into three classes: social (all affiliative behaviors), agonistic (all aggressive behaviors), and socio-sexual (all directly reproductive behaviors) (Supplementary A). All social behaviors included directionality (give versus receive) and which party (focal or social partner) initiated or terminated an interaction, if the initiation and/or termination was directly observed. We also recorded information regarding the social partner. This information included, when possible, the partner's age-sex classification and their individual identification. It was not always possible to positively identify social partners due to a number of factors including rapidity of interaction, visual obstruction, or fading of identifying dye-markings.

Data collection resulted in a total of 512.5 hours of behavioral data with approximately equal effort across males within study periods.

V.II.III. Data Analysis

We assessed the impact of three demographic variables on sociality from two perspectives: individual behavioral trends and social networking. The first was rank, which was assessed on a categorical (high, middle, low) basis and had been previously established from behavioral data (Gartland et al., 2020). The second variable was age (yrs) and the third variable was age-class which divided individuals into adult (>7-15 yrs) and aged (>15 yrs) (Hamada & Yamamoto, 2010) (Table 5.2). This allowed us to compare whether an individual being in their biological prime *versus* being past prime impacted their sociality and positionality.

Data was collected in 11-hour sets. For each 11-hour period, we calculated behavioral rates as the number of observations of a specific behavior divided by the total number of observation points. Specific behaviors were: affiliation received, affiliation given, mutually-directed affiliation, affiliation with adult females, affiliation with subadult males, affiliation with adult males, affiliation with juveniles, affiliation with infants, affiliation with males, affiliation with females, aggression received, aggression given, aggression with adult females, aggression with subadult males, aggression with adult males, aggression with juveniles, aggression with infants, aggression with males, and aggression with females. Affiliation and aggression with males included male individuals from all age classes, as did affiliation and aggression with females. Affiliative behaviors included grooming, huddling, playing, ventro-social contact, and other positive social interactions. Aggressive behaviors included chasing, threat displays, biting, displacements, and other contact aggression.

One-way ANOVAs were used to establish which of the sociality variables contained significant variation between individuals. Nested ANOVAs with individuals nested within rank and age-class subgroups, were used to examine whether there was variation in a given sociality variable (1) between age classes and ranks and (2) between individuals within age class and ranks.

The social network was constructed from behavioral data. This involved identifying all data points in which a focal male had an affiliative interaction with another identified individual within the group. From the resulting network, we calculated the following social networking measures: degree, betweenness, closeness, and eigen value for each focal male. These measures are often correlated with each other, as focal subjects with high degree are likely to have correspondingly high closeness and betweenness (Wey et al., 2008). Individuals AM1, AM4, AM6, and AM11 were not included in social network analyses due to insufficient data points with identified social partners.

A Pearson's correlation was used to examine the relationships between demographic variables and sociality and centrality measures. As all behavioral categories are independent and non-overlapping, tests are therefore orthogonal and do not require non-orthogonality corrections (e.g. Bonferroni) (Sokal & Rohlf, 2012). Our social network analyses were conducted using the igraph package in R (Csardi & Nepusz, 2006). All one-way ANOVAs, nested ANOVAs, and Pearson's correlations were run in SAS ©, 9.4.1 (Cary, NC, USA).

V.III. Results

Results of the one-way ANOVAs examining individual variation in sociality variables were similarly largely significant across the board (Table 5.3). The only variables in which individuals did not significantly vary from each other were affiliation with infants, aggression with adult males, aggression with subadult males, and aggression with males (Table 5.3).

Table 5.3. One-way ANOVA results for sociality variables.

Sociality Variable	**F**	**Df**	**P**	**Significant?**
Affiliation				
Mutual	2.49	16	<0.002	Y
Give	4.35	16	<0.001	Y
Receive	3.06	16	<0.001	Y
Adult Females	4.19	16	<0.001	Y
Adult Males	4.28	16	<0.001	Y
Subadult Males	6.26	16	<0.001	Y
Juveniles	5.66	16	<0.001	Y
Infants	0.76	16	0.7338	N
Males	3.88	16	<0.001	Y
Females	3.59	16	<0.001	Y
Aggression				
Give	3.15	16	<0.001	Y
Receive	3.82	16	<0.001	Y
Adult Females	2.15	16	<0.01	Y
Adult Males	1.39	16	0.1506	N
Subadult Males	1.03	16	0.4285	N
Juveniles	1.83	16	<0.05	Y
Infants	1.84	16	<0.05	Y
Males	1.28	16	0.2136	N
Females	2.32	16	<0.01	Y

The results of the nested ANOVAs are presented in Table 5.4.1 and Table 5.4.2.

Table 5.4.1 Results of nested ANOVAs for Dominance Rank.

Sociality Variable	Dominance Rank					
	Between Subgroups			Within Subgroups		
	F	df	P	F	df	P
Affiliation						
Mutual	0.63	2	0.54	2.17	17	<0.01
Give	1.13	2	0.35	3.67	17	<0.001
Receive	0.62	2	0.55	2.82	17	<0.001
Adult Females	0.85	2	0.45	4.75	17	<0.001
Adult Males	2.21	2	0.14	3.20	17	<0.001
Subadult Males	0.89	2	0.43	10.0	17	<0.001
Juveniles	1.25	2	0.31	5.57	17	<0.001
Infants	1.26	2	0.31	0.61	17	0.88
Males	2.47	2	0.11	3.47	17	<0.001
Females	1.02	2	0.38	3.85	17	<0.001
Aggression						
Give	6.01	2	0.01	1.94	17	<0.05
Receive	1.26	2	0.31	3.08	17	<0.001
Adult Females	4.25	2	0.03	1.85	17	<0.05
Adult Males	0.31	2	0.74	5.26	17	<0.001
Subadult Males	1.61	2	0.23	0.83	17	0.65
Juveniles	4.16	2	0.03	1.78	17	<0.05
Infants	2.20	2	0.14	1.35	17	0.17
Males	0.29	2	0.75	3.82	17	<0.001
Females	4.24	2	0.03	1.94	17	<0.05

Table 5.4.2 Results of nested ANOVAs for Age Class.

Sociality Variable	**Age Class**					
	Between Subgroups			**Within Subgroups**		
	F	**df**	**P**	**F**	**df**	**P**
Affiliation						
Mutual	0.79	1	0.39	2.53	15	<0.01
Give	2.25	1	0.15	4.03	15	<0.001
Receive	0.07	1	0.80	3.25	15	<0.001
Adult Females	0.12	1	0.73	4.43	15	<0.001
Adult Males	0.04	1	0.85	4.55	15	<0.001
Subadult Males	0.68	1	0.42	6.39	15	<0.001
Juveniles	1.64	1	0.22	5.44	15	<0.001
Infants	0.88	1	0.36	0.76	15	0.72
Males	0.07	1	0.80	4.12	15	<0.001
Females	0.06	1	0.81	3.81	15	<0.001
Aggression						
Give	5.25	1	0.04	2.49	15	<0.01
Receive	0.30	1	0.60	3.99	15	<0.001
Adult Females	1.96	1	0.18	2.03	15	<0.05
Adult Males	1.34	1	0.26	1.36	15	0.17
Subadult Males	0.92	1	0.35	1.03	15	0.42
Juveniles	13.60	1	<0.01	1.02	15	0.43
Infants	3.89	1	0.07	1.56	15	0.09
Males	2.11	1	0.17	1.20	15	0.28
Females	3.71	1	0.07	1.98	15	<0.05

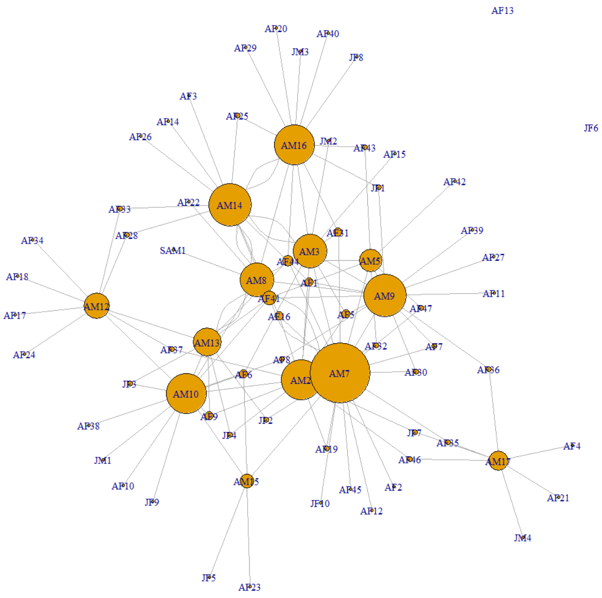
Individuals had a degree range of 5 to 21 (Table 5.5). The individual with the highest degree, closeness, betweenness, and eigenvalues was AM7 who is neither the dominant male nor currently listed within the “high” dominance rank category (Table 5.5). There were differences in social clustering by which some males have reciprocal relationships with each other (i.e. AM14 and AM16), while others are only weakly tied into the core males through shared social partners (i.e. AM17) (Fig. 5.1). From this analysis, we can also identify non-focal individuals such as AF1 and AF41 who maintain centralizing relationships with multiple adult males (Fig. 5.1).

Table 5.5. Individual centrality measures.

Individual	Degree	Closeness	Betweenness	Eigen Value
AM2	14	0.003226	477.7653	0.6560001
AM3	12	0.003257	353.4423	0.8329279
AM5	8	0.003030	145.6462	0.3557083
AM7	21	0.003300	761.2399	1.0000000
AM8	12	0.003300	461.3747	0.9539569
AM9	15	0.003185	448.9009	0.6499391
AM10	14	0.003185	504.9497	0.4817723
AM12	9	0.002762	323.6948	0.1829497
AM13	10	0.003012	183.3883	0.4983149
AM14	15	0.003039	403.4094	0.8324227
AM15	5	0.002941	159.9693	0.2204659
AM16	14	0.003003	425.7681	0.6305065
AM17	7	0.002519	218.0443	0.0540503

The Pearson's correlation between demographic variables, sociality variables, and centrality measures revealed a number of significant relationships, particularly between directed behaviors (Table 5.6). An individual's dominance rank was negatively correlated to their rate of affiliation with adult males, subadult males, and juveniles as well as their rate of aggression given and aggression with adult females, juveniles, and infants (Table 5.6). An individual's age was positively correlated to their rate of affiliation given and affiliation with juveniles as well as their rate of aggression given and aggression with adult females, juveniles and infants (Table 5.6).

Figure 5.1 Representation of study subjects within the social network.



Some social variables including rate of aggression given, rate of affiliation with juveniles, and rate of aggression with females significantly correlated to all three demographic variables in different ways. For example, rate of aggression with females was negatively correlated with both dominance rank and age class, but positively correlated with age (Table 5.6). All measures of centrality were significantly negatively correlated to dominance rank and significantly positively correlated with affiliation with adult males. The number of social partners an individual had (degree) was positively correlated with affiliation given, affiliation with adult females, affiliation with infants, and affiliation with females while being negatively correlated with affiliation with subadult males, affiliation with juveniles, aggression received, and aggression with subadult males (Table 5.6). An individual's eigen value (centrality relative to other individuals in the network) was positively correlated to age, affiliation given, affiliation with adult males, affiliation with subadult males, affiliation with males, and aggression given while being negatively correlated with aggression received and aggression with subadult males (Table 5.6). There were not enough data points to successfully run a correlation of aggression with infants against the centrality measures (Table 5.6).

Table 5.6. Correlations between demographic variables, sociality variables and centrality measures.

Sociality Variable	**Rank**			**Age**			**Age-Class**		
	R	**N**	**P**	**r**	**N**	**P**	**R**	**N**	**P**
Affiliation									
Mutual	-0.11	191	0.14	0.13	191	0.07	-0.10	191	0.18
Give	-0.10	191	0.15	0.19	191	<0.01	-0.19	191	<0.01
Receive	-0.12	191	0.09	0.03	191	0.69	-0.03	191	0.67
Adult Females	0.04	191	0.60	0.06	191	0.45	-0.05	191	0.52
Adult Males	-0.23	191	<0.001	0.03	191	0.65	0.03	191	0.71
Subadult Males	-0.19	191	<0.05	-0.12	191	0.13	0.13	191	0.08
Juveniles	-0.22	191	<0.01	0.18	191	<0.05	-0.18	191	<0.05
Infants	-0.04	191	0.60	-0.02	191	0.74	0.06	191	0.41
Males	-0.25	191	<0.001	0.02	191	0.79	0.03	191	0.64
Females	0.04	191	0.63	-0.05	191	0.46	-0.03	191	0.67
Aggression									
Give	-0.30	191	<0.001	0.24	191	<0.001	-0.24	191	<0.001
Receive	0.14	191	<0.05	-0.05	191	0.50	0.07	191	0.33
Adult Females	-0.23	191	<0.001	0.16	191	<0.05	-0.14	191	0.06
Adult Males	0.02	191	0.81	-0.09	191	0.19	0.10	191	0.18
Subadult Males	0.11	191	0.12	-0.07	191	0.36	0.07	191	0.33
Juveniles	-0.22	191	<0.01	0.26	191	<0.001	-0.26	191	<0.001
Infants	-0.14	191	<0.05	0.26	191	<0.001	-0.26	191	<0.001
Males	0.07	191	0.35	-0.11	191	0.12	0.11	191	0.12
Females	-0.25	191	<0.001	0.20	191	<0.01	-0.19	191	<0.01
Centrality									
Degree	-0.17	136	<0.05	0.04	136	0.67	0.10	136	0.30
Closeness	-0.72	136	<0.001	0.40	136	<0.01	-0.27	136	<0.01
Betweenness	-0.30	136	<0.001	0.18	136	<0.05	0.18	136	<0.05
Eigen Value	-0.48	136	<0.001	0.18	136	<0.05	-0.07	136	0.40

V.IV. Discussion

The goal of this study was to assess the impact of male demography on sociality as measured both by behavioral trends and social network measures from a biological market framework. Our initial one-way ANOVAs established that individuals differ significantly in their sociality (Table 5.3). The only non-significant affiliation variable was affiliation with infants, but there was limited data as there were very few interactions between males and infants. It is interesting that there was no significant variation in aggression with adult males, subadult males, and males. This is consistent with a dominance structure driven by social skill rather than aggression.

The results from the nested ANOVAs demonstrate that, for affiliative variables, there is no significant behavioral variation between dominance ranks or between age classes. However, excluding affiliation with infants, there is significant variation between individuals within dominance ranks and age classes for all affiliative behaviors. The lack of between-group variation in affiliative variables suggests that these behaviors, and the rates at which individuals engage in them, are more individually-driven and not rank or age-class strategy.

The same is not consistent for aggressive variables. There is significant variation between both dominance rank and age class subgroups in aggression given and in aggression with juveniles (Table 5.4). There is also significant variation between individuals within dominance rank and age class subgroups for a number of aggressive variables. These results would conform with the general theory of dominance as selecting for fighting availability and this ability decreasing as an individual moves from prime adulthood into agedness (Alberts et al., 2003; Bernstein, 1976; Coleman et al., 2011;

Cowlishaw, 1991; de Ruiter, 1993; Watts, 2010). Thus, the nested ANOVA results for these aggression variables might lead one to conclude that higher ranking males display significantly more aggression than middle or lower-ranking males.

However, studies of Japanese macaques have noted the importance of group tenure and other social skills over physical condition in securing high rank (Eaton, 1976; Takahashi, 2002; Takahata et al., 1999). The importance of age (potentially as a measure of experience) and tenure in Japanese macaque society would explain the strong relationship between the age class and dominance variables. This is further supported by the correlation results. Dominance rank was significantly negatively correlated with all measures of centrality as well as affiliation (particularly with males) and aggression (particularly with females) (Table 5.6). These results suggest that as an individual's rank increases, his affiliative efforts with other males decreases.

This could be explained as a biological market. As the male gains rank, and thus increases his value as a trading partner on the biological market, his need to curry favor with other males decreases. As such, he no longer exerts the same affiliative effort towards other males as there is little benefit. This is supported by the negative correlation between age class and affiliation given, particularly as age class is closely related to dominance rank as a function of group tenure as previously discussed. We also see this reflected in the centrality results. Dominance rank was significantly negatively correlated with all measures of centrality (Table 5.6). This suggests that high-ranking males are able to identify a few key relationships to maintain which serve to protect their own rank security. It could also be that, due to the benefits conveyed by rank and resultant positionality within the biological market, it is not necessary for these high-ranking males to maintain high network centrality in order to maximize their resource access.

We can also see support for this perspective on demography from the significant positive correlations between age and affiliation given, affiliation with juveniles, aggression given, aggression with adult females, aggression with juveniles, aggression with infants, and aggression with females of all age classes (Table 5.6). If male rank is tied to group tenure, then younger males with a shorter tenure should need to exert more social effort in order to barter and trade on the biological market. This is reflected in higher rates of affiliation as individuals age, with effort likely reaching a plateau and/or beginning to decrease at some point after 15yrs when males are both “aged” and have attained the requisite group tenure to ensure high rank. There is also a positive correlation between age and both closeness and eigen value. Younger, maturing males still establishing their group tenure may need to exert greater social effort and remain closely connected to the greater group network in order to access key resources.

Our results demonstrate a significant relationship between demography and sociality. In the case of dominance, the two prime conflicting theories of dominance as selecting for fighting ability or selecting for social skill should mean that we see a significant relationship between dominance and aggression and/or dominance and affiliation/social centrality. However, neither of these predictions holds true. Instead, we see a complex interplay between dominance and age whereby agedness or “experience” and/or group tenure confer individual status. Rather than seeing males increase their aggressive efforts or their affiliative efforts as rank increases, we see a negative relationship between these variables. Rather, these data suggest that young “prime” males exert increasing affiliative social efforts, but reach some plateau which results in insignificant variation in affiliation between age classes.

CHAPTER VI

SUMMARY REMARKS

The objective of this dissertation was to examine varying social strategies in adult male Japanese macaques. The following conclusions can be drawn from the results of the studies presented in Chapters III, IV, and V:

1. Dominance in adult males is highly contextual and hierarchical position can vary significantly depending on whether methodological approach favors aggressive interactions, affiliative interactions, or priority-of-access.
2. Centrality between adult males is not solely dependent on dominance rank, as middle-ranking individuals can hold pivotal spaces within the social network. As such, social centrality is a factor which should be utilized in partnership with dominance rank when making group management decisions.
3. Differences in aggressive behavioral strategies have a significant impact on both dominance rank and reproductive success such that more aggressive males hold higher rank, but have lower reproductive success than less aggressive males. Variation between affiliative and aggressive strategies and individual clustering point to alternative mating strategies in operation within this population.
4. Affiliation, particularly with other males, decreases as male rank and age increases. Similarly, male rank is negatively correlated with every measure of network centrality. Based on a biological market approach, older dominant males exert less social effort and maintain fewer strong connections than

younger lower-ranking males. We suggest that this difference is explained by the difference in ability to monopolize commodities and secure high-value trading partners between males of high and mid or low rank.

APPENDIX

DATA SHEET

Japanese Macaque Male Sociality Study

Time	**Behavior**	**Modifier**	**G/R**	**Notes**	**Partner Sex**	**Partner Code/ID**	**Natal (Y/N)**	**I/T - ID**
0:00								
1:00								
2:00								
3:00								
4:00								
5:00								
6:00								
7:00								
8:00								
9:00								
10:00								
11:00								
12:00								
13:00								
14:00								
15:00								

Focal ID:______________ **Date:_________________** **Time:_____________**

Dye Mark:_____________ **Age Class:_____________** **Entered:____**
Observer:________

Possible Non-Adult Male Partners:
J – Juvenile (0-4yrs)
SA – Subadult (>4-7yrs)
A – Adult
UK - Unknown

NOTES

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