Contra-hierarchical aggression among female rhesus macaques (*Macaca mulatta*)

By

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B.S. (University of California at Davis) 2008

THESIS

Submitted in partial satisfaction of the requirements for the degree of

MASTER OF SCIENCE

in

Animal Biology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

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Abstract

Among rhesus macaques, bi-directional aggression may occur between animals with shifting or ambiguous ranks, or between those whose relative ranks are well established. Factors that influence the latter case (here termed "insubordinate aggression") are not well understood. These factors are of interest because insubordinate aggression may be associated with stability in dominance relationships, and stability in dominance relationships is critically related to group stability. We hypothesized that in well-established female dominance relationships, the likelihood of insubordination during conflicts is influenced by characteristics of both opponents. Multivariate analysis of 11,591 dyadic conflicts among females in six captive rhesus groups shows that dyadic and individual characteristics related to weight, rank, age, and access to social support affect the likelihood of insubordinate aggression. As expected, insubordinate aggression is less likely to occur among dyads with high disparity in weight. The effects of age, rank, and access to social support are more complex. Increasing subordinate age is associated with increased modulation of insubordinate aggression according to opponent age. Age-based deference, i.e. suppression of insubordination associated with opponent age, decreases with increasing age of the lower-ranking opponent. Similarly, dyadic rank disparity has different effects on insubordination rate according to the age of the subordinate opponent. As females age, their likelihood of insubordination is less dependent on the degree to which they are outranked by their opponent. Also, the lower-ranking opponent's level of social support significantly affects her likelihood of insubordination, but the dominant animal's level of social support does not affect her likelihood of receiving insubordination. We predicted that for the lower-ranking opponent, having many maternal kin would promote insubordinate behavior, whereas for the higher-ranking opponent, having many maternal kin would inhibit insubordination. However, our results show that the dominant's matriline size has no effect on her likelihood of receiving insubordination. Further, matriline size has the opposite of the predicted effect for subordinates—subordinates with many maternal kin are significantly less likely to be insubordinate than those with few kin. We propose some possible explanations for this, which will require further investigation. Taken together, this research suggests that females gauge their degree of deference to dominants based on their own characteristics relative to their opponent's, taking into account size, age and weight differences as well as their own access to social support. Features of subordinate animals emerge as more important than those of dominants in determining the likelihood of insubordinate aggression in dyadic conflicts. Understanding determinants of insubordination will contribute to management practices aimed at maintenance of group stability, as the ultimate act of insubordinate aggression—social overthrow—poses a major welfare and management problem.

CHAPTER 1: Literature Review

1.1 Background

This work is an exploration of individual decision-making in dyadic conflicts among female rhesus macaques. I investigate factors that predict contra-hierarchical (here termed "insubordinate") aggression, which is a decision that sometimes results in dramatic structural upheaval in rhesus social networks. The question of why female rhesus macaques decide to engage in insubordinate aggression is interesting in an applied sense because the most extreme outcome of this behavior, social overthrow, is a frequent and financially costly hazard of group-housing rhesus macaques in captivity (McCowan et al., 2008; Oates-O'Brien et al., 2010). It is also an interesting evolutionary question, because the processes by which group-living individuals negotiate and exercise power have an important role in the evolution and stability of social groups. In this chapter, I will provide the biological background and evolutionary theory that form the foundation of this work, beginning with an overview of macaque biology followed by a review of competition, sociality, and power among primates and ending with a discussion of the application of this work in captive rhesus management.

1.2 Macaques: an Overview of Phylogeny, Biology, and Behavioral Ecology

Macaques are among the most adaptable, resilient, and opportunistic of Old World monkey genera, allowing them to thrive in the unpredictable conditions of the modern era. They have the widest range of any primate genus save man, and are found throughout East and Southeast Asia, Afghanistan, India, and in parts of North Africa (Fooden, 1980). Macaque species occupy a variety of ecological niches ranging from tropical forests to cold montane forests to urban areas, and have diverse and varying diets (Napier & Napier, 1985). There are currently considered to be sixteen extant macaque species (Thierry et al., 2004). All of these species are semi-terrestrial quadrupeds that show female philopatry and male dispersal, with males dispersing from and females remaining in their natal groups. Groups are typically comprised of several maternally-related family units, or matrilines, which generally occupy separate dominance rank tiers and form the core of the group. Beyond these fundamental similarities, macaque species exhibit a great deal of interspecific diversity in temperament and patterns of social behavior. Thierry (2004) classified macaque species according to a four-grade scale of social behavior, with despotic species, characterized by rigid linear dominance hierarchies and frequent, severe aggression, as grade one, and tolerant species, which have egalitarian societies with minimal aggression, as grade four. Social style appears to map well onto phylogenetic relationships. The most prolific macaque species, rhesus macaques (*Macaca mulatta*), long-tailed macaques (*Macaca fascicularis*), and pig-tailed macaques (*Macaca nemestrina*), fall into grades one or two, suggesting that the characteristics that lead to despotism and intolerance also give macaque species a competitive advantage.

Rhesus macaques are the most intolerant and despotic of macaques, and the most widespread of all non-human primate species (Thierry, 2004). They form multi-male, multi-female groups that can be variable in size, ranging from 10-80 individuals (Melnick et al., 1984; Teas et al., 1980). Rhesus macaques are ubiquitous in southern China and India, and are also found in South East Asia, Pakistan, and Afghanistan. They are of major importance as pests that cause crop damage, disorder, injury, and disease, and as the major non-human primate biomedical model, utilized in research laboratories worldwide (Animal and Plant Inspection Service, 2010).

Life History of Rhesus Macaques

Rhesus macaques are seasonal breeders, tending to give birth in the spring to maximize resource availability for lactating mothers and infants. Since gestation is about 165 days (5 ½ months), breeding season takes place during fall. Prior to ovulation, females begin to engage in "consortships," during which a female will select a mate and remain in close proximity to him for several days, grooming, huddling, and intermittently copulating. Rhesus macaques are a multiple-mount species; males ejaculate only after a sequence of separate intromissions occurring over a 5-30 minute period (Dewsbury & Pierce 1989). Pairs often exhibit heightened aggressiveness towards group members during consortships. In addition, dominant males frequently disrupt the consortships of lower ranking males through aggression towards either member. Thus, mating among macaques can be accompanied by heightened rates of aggression and trauma.

Females reach sexual maturity between 3-4 years old in the wild (Drickamer, 1974) and between 2-3 years old in captivity, likely due to better nutrition in captivity (Small, 1981). Achievement of reproductive maturity is often marked by reddening and swelling of a female's rump, hind legs, and forehead (Soltis, 2004). A female may give birth at age three or four, and since gestation lasts about 5 ½ months and infants may be weaned at 6 months, a female can potentially give birth every year. However, interbirth intervals vary between individuals and over a female's reproductive lifetime. Interbirth intervals tend to shorten if a female's current infant dies and lengthen if the infant lives, especially if the infant was born late in the birth season. In captivity, 70-80 percent of reproductively active females give birth during an average season. Female rhesus experience reduction of fecundity starting at around age 20, characterized by longer interbirth intervals and reduced sexual activity (Bercovitch & Harvey, 2004). This perimenopausal period culminates in cessation of reproductive capacity by about age 25. Post-menopausal rhesus have endocrine profiles very similar to those of post-menopausal human women, but the adaptive benefit of menopause in macaques is unclear, as it is exceedingly rare for wild females to live to post-menopausal age (Bercovitch & Harvey, 2004). In captivity, female rhesus may live to between 25-30 years of age; thus, a female that lives to menopausal age may be capable of birthing 15 or even 20 offspring. However, even in captivity infant death rates are quite high—about one in ten infants die before they are one year old and three in ten before they reach one year old (Bercovitch & Berard, 1993).

Male rhesus reach puberty at around age three and begin to undergo physiological and behavioral changes such as growth of long canines, descent of enlarged testes, and motivation to emigrate from their natal group (Bercovitch & Harvey, 2004). Duration of the maturation phase (i.e. the interval between development of reproductive capacity and growth to full adult body weight) is longer for male rhesus than for females—four to six years as opposed to about three years. This is perhaps because of greater disparity between immature and mature body mass, and/or to allow males time to develop the behavioral repertoire necessary for competitive and reproductive success (Thierry et al., 2004). Typically, males disperse from their natal group after reaching reproductive competency but before reaching full adulthood, usually between the ages of four and six (Rawlins & Kessler, 1986). Emigrating males may immediately seek to enter a new group or may live outside of a breeding group for some time, sometimes with a small group of fellow emigrants. Rhesus males usually enter new groups during the breeding season, and entry is facilitated by social interactions with females. Existing group males typically allow new males to enter the group in the lowest hierarchical position but attempt to aggressively monopolize mating opportunities. Females may not be monopolized against their will, however, and females prefer to mate with novel males. Because of this, length of male tenure in a troop is negatively correlated with reproductive success, so males may transfer to new troops several times throughout their lives in an attempt to maximize breeding opportunities (Soltis, 2004). Differential success at joining new groups and increased risk of death during inter-group transfer leads to heightened death rates among male rhesus compared to females. Further, many males spend considerable periods living outside of groups, or in bachelor groups (Paul & Kuester, 1985). Thus, wild groups typically have skewed adult sex ratios of about four females to every male (Bercovitch & Harvey, 2004).

1.3 Balancing Cooperation and Conflict: the Evolution of Macaque Social Behavior

Gregarious primates such as rhesus macaques form stable groups despite the conflict that often results from grouping (Janson 1988)[1]. It can be inferred that for gregarious primate species, the benefits of grouping, such as reduced risk of predation and infanticide or better defense of clumped resources, have generally outweighed the associated costs of grouping over evolutionary time (Smuts & Smuts, 1993; Sterck et al., 1997; van Schaik, 1989; Wrangham, 1980)[2]. Many primate species have developed a variety of social adaptations that help to ameliorate and mitigate conflict that arises, thus aiding the maintenance of stability. Three such mechanisms of conflict management that are especially pertinent to this research are female social philopatry, dominance hierarchies, and nepotism.

Kinship and Competition

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[1] A challenge to the assumption that grouping inevitably leads to intra-group conflict is presented by Isbell & Young (2002), who point out that many colobine species group together without apparent “cost”.

[2] Phylogenetic constraints and founder effects may also be crucial in determining the nature of primate societies (Di Fiori & Rendall, 1994)

A majority of gregarious primates show female philopatry, wherein females remain in their natal area, and male dispersal, wherein males emigrate to unrelated groups (a mechanism of inbreeding avoidance) (Sterck et al., 1997). Isbell and Van Vuren (1996) proposed that female philopatry may have evolved through a two-step process. Firstly, the dangers of leaving the natal area (e.g. unfamiliar conditions, competition with unknown others, and predation) may have lead to selection for locational philopatry (i.e. remaining in the natal area). Secondly, once generations of females began occupying the same area, it may have been to their advantage to engage in social philopatry (Isbell & Young, 2002). Inclusive fitness, anti-predator benefits, infanticide avoidance, and increased ability to monopolize and usurp food from outsiders may all confer reproductive advantages to females that group and cooperate together (Dunbar, 1988; Isbell, 1994; Janson, 1988). Although males stand to gain the same benefits from philopatry as females, they are more frequently the emigrating sex (Harcourt, 1978; Pusey, 1992). This is likely because female reproductive success is limited by access to food, whereas male reproductive success is limited by access to females; therefore, female social organization is largely determined by food availability, whereas mating opportunities may be more important in determining male social behavior (Clutton-Brock, 1988; Di Fiore & Rendall, 1994; Emlen & Oring, 1977; Trivers, 1972).

The nature of within-group competition over food is primarily determined by the availability and distribution of this resource (Isbell, 1991; Isbell & Young, 2002; Janson, 1988; Sterck et al., 1997; van Schaik, 1989; van Schaik & van Noordwijk, 1988; Wrangham, 1980). Features of food distribution that are important in determining the nature of competition include its monopolizability (i.e. the degree to which others can be excluded from obtaining access) and its usurpability (i.e. the potential for resource takeover) (Isbell & Young, 2002).

Within-group competition over food can be described either as primarily ‘scramble’, in which food is neither monopolizable or usurpable, or primarily ‘contest’, in which food is monopolizable and usurpable, leading to frequent conflict (Janson & Van Schaik, 1988; Van Schaik & Van Noordwijk, 1988). The socioecological model proposed by Wrangham (1980) and adapted by Sterck et al. (1997) predicts that species adapted to cope with scramble-type within-group competition are likely to have egalitarian social structure, characterized by few agonistic interactions and absence of strong dominance structure. In these societies, the costs of grouping may be relatively low. Conversely, in species evolved to exploit monopolizable, usurpable food types, group-members may come into conflict over resources more frequently. Under such circumstances, costs of grouping are high; however, they may be offset by the benefits provided by competitive advantage in between-group competition. Further, a variety of evolved mechanisms may serve to promote group stability and conflict mitigation, lessening the deleterious effects of conflict.

Coping with Competition: Dominance Hierarchies, Nepotism, and Coalitions

In addition to being offset by the benefits of inter-group competitive advantage, grouping costs are ameliorated through a variety of socio-behavioral mechanisms. Investigation of specific behavioral mechanisms through which costs of within-group competition are mitigated is ongoing, and many factors have been identified (e.g. grooming: Barrett et al., 1999; policing: Flack et al., 2006; kinship: Beisner et al., 2011). Here I will discuss two of the most basic socio-behavioral adaptations that promote group stability in the face of intra-group contest competition: kin alliances and dominance hierarchies.

When faced with high within-group contest competition, females are expected to form alliances with kin, benefitting from both inclusive fitness and the competitive advantage provided by coalitionary support (Hamilton, 1964; Silk, 2002). These kin alliances aid in ameliorating some of the costs of contest competition by promoting cooperation and altruism between related females living in groups (Silk, 2002). For many primate species, including rhesus macaques, matrilineal associations form the basis of social organization: the advantages conferred by nepotism lead to the formation of maternally related subgroups (matrilines) comprised of closely bonded females. Maternally related kin preferentially provide each other with coalitionary support (Berman, 1980; de Waal, 1977; Kaplan, 1978; Silk, 1982), affiliation (Missakian, 1974; Sade, 1965; Silk et al. 1981), increased tolerance during feeding (de Waal, 1986a), and increased reconciliation after conflicts (Bernstein, 1991). All of these nepotistic behaviors help to alleviate conflict, promote social cohesion, and establish matrilineal structure as the foundation of many primate societies.

Another mechanism of coping with strong intra-group contest competition is the formation of dominance hierarchies. Hierarchies are beneficial in general because competitive ability is variable among individuals but fairly consistent for individuals in their prime; permanent group members who repeatedly face each other in contests over food may consistently win against some group mates and lose against others (Jones, 1981; Wilson, 1975). Under such conditions the formation of formal dominance hierarchies—wherein weaker individuals submit without contest to stronger individuals, often using formalized signals to avoid aggression—can help alleviate the costs of contest competition (de Waal & Luttrell, 1989).

In female-bonded societies, nepotism shapes hierarchical structure. Of key importance is the consistent, aggressive maternal support of infants. Through repeated maternal intervention and protective behavior, infants develop dominance over every animal their mother is dominant to, at first indirectly through the mother, then directly as the infant matures (Berman, 1980; de

Waal, 1977; de Waal & Luttrell, 1986). This leads to offspring acquiring the rank immediately below their mothers. Thus, over generations, highly structured matrilineal dominance hierarchies are built, wherein most or all members of a matriline occupy adjacent ranks and separate matrilines occupy distinct ranks relative to each other[3]. In female-bonded species, since males emigrate at puberty and may move between groups multiple times in their lifetimes, male and female hierarchies are largely independent, with the female hierarchy functioning as the stable core of group structure.

Dominance hierarchies may be strongly or weakly expressed. Strongly expressed hierarchies are usually observed in female-bonded, nepotistic societies (Isbell & Young, 2002; Wrangham, 1980). This is because the conditions associated with female philopatry and nepotism (high levels of within-group competition) promote frequent conflict. When conflict is frequent, dominance is frequently reinforced, leading to 'strong' hierarchies in which dyadic dominance relationships are typically unambiguous and enforced with aggression (Isbell & Pruetz, 1998). In contrast, weakly expressed hierarchies are typically observed in egalitarian societies, in which conflict is rare (Mitchell et al., 1991; Sterck & Steenbeck, 1997) .

Rhesus macaques are described as the most despotic of macaques (Thierry, 2004), characterized by strong, stable dominance hierarchies reinforced with frequent unidirectional aggression. Among rhesus, then, access to food is strongly mediated by rank, with dominant females capable of monopolizing food resources and aggressively excluding subordinate animals from access. Low-ranking females in many species have been shown to suffer reproductive costs, likely due to reduced access to resources. Low-ranking females have been observed to

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[3] Fushing et al. (2011) present evidence that hierarchical structure is better described as 'corporative' rather than linear, with multiple individuals able to occupy the same rank tier. However, linear hierarchies can provide information about dyadic rank relationships, taking into account that some dyads may not have dominance asymmetry.

have longer inter-birth intervals, less robust infants, and take longer to reach sexual maturity (Harcourt, 1987; Silk, 2002; Van Schaik & Van Noordwijk, 1988). This results in a cost-benefit disparity between high- and low-ranking female macaques; while both high- and low-ranking females potentially obtain the same anti-predator benefits from grouping, high-ranking females stand to benefit much more from the competitive advantage in between-group conflicts that is provided by the support of low-ranking females than vice versa. In other words, the likelihood of winning against other groups is increased by the presence of each adult female in the group, but the reward for winning contests with other groups can be effectively monopolized by dominant individuals within the group. It has been suggested that dominant females should show tolerance and give concessions if they "need" lower ranking animals to stay in the group because of high between-group contest competition (Sterck et al., 1997; Dietz, 2004). On the flip side, low-ranking females may be more likely to act in opposition to the existing social order, because they have more to gain than dominant females. Subordinate animals can either tolerate or reject the social impositions of dominant animals, presumably based on their estimation of the potential costs and benefits of doing so. This could potentially explain why, in a number of female philopatric species, group transfer by females (Moore, 1984) and group fission (Dittus, 1988) are occasionally observed.

Stability, Opportunity, and Risk: Responding to Changing Opportunities

Even the most rigid societies must be able to accommodate shifting social and environmental conditions. Otherwise, inevitable change (e.g. morbidity or mortality of group-members) could destroy social order. In addition, it can sometimes be in the best interest of individual group-members to initiate social change. Dominance hierarchies are the main organizing principle of many primate societies. The ease with which hierarchical change occurs in is affected by patterns of tolerance and despotism. Despotism inhibits hierarchical flexibility, because it increases the risk individuals face when attempting to ascend in rank, by increasing potential punishment inflicted by dominants. However, despotism also increases the costs associated with being low-ranking, thereby increasing the value of ascending in rank. Thus, high pressure imposed on subordinates by dominants (e.g. through social aggression and resource monopolization) could affect their likelihood of rebellion in two opposite ways, either inhibiting it though punishment, or encouraging it by driving pursuit of relief. In macaque societies, the balance between risk of punishment and opportunity for increasing fitness through social betterment becomes the crux of subordinate decision-making. This research attempts to illuminate this decision-making process, with particular attention to the factors that drive females to engage in insubordinate behavior. The goals of this research are to 1) determine what properties of dyadic relationships are likely to encourage insubordinate aggression, and 2) increase understanding of the processes by which power dynamics fluctuate in a rigidly hierarchical society.

Social Overthrows

Insubordinate aggression is of interest because it can precipitate dramatic social upheavals known as "social overthrows". These events are seemingly spontaneous eruptions of severe contra-hierarchical aggression (McCowan et al., 2008) in which a number of animals are often killed. Although males are usually involved in these conflicts, sometimes playing central roles, social overthrows are, at their core, a female affair. Most commonly, matrilines are pitted against each other, and the most dominant matriline is often attacked by a coalition of several lower ranking matrilines (Oates-O'Brien et al., 2010).

The causes of these social overthrows are complex and poorly understood. Many hypotheses have been put forth, but overall the circumstances surrounding documented overthrows have proven inconsistent—no one factor has been consistently linked to overthrows. Overthrows are more frequent in captivity, which suggests that some factor(s) associated with captivity may play a causal role. One major reason for this is that when social order is strained beyond repair, there are only two potential outcomes: major conflict or group fission/disbanding. In the wild, social instability sometimes results in fissioning (Dittus, 1988). In captivity, however, group fission is not a possible response, therefore irreconcilable conflict can only be resolved through aggression.

Among captive groups, there is considerable heterogeneity in the levels of aggression and the frequency of severe aggressive outbreaks; some groups may remain stable and relatively peaceful for decades, while other groups develop acute social instability, which manifests as abnormal trauma patterns and/or social overthrows. McCowan et al. (2008) found that social overthrows were associated with several social network measures: low grooming reciprocity, low average social power (subordination degree: rate of subordination signals received and diversity of signalers), and high fragmentation in displacement networks (reflecting more ambiguity surrounding dominance relationships). These findings indicate that detectable social instability precedes social overthrows. However, proximate social perturbations, likely in combination with pre-existing social instability, often appear to foment social upheaval. For example, removal of the dominant male or female has been identified as a contributing factor (Oates-O'Brien et al., 2010), along with maturation of key females (Samuels & Henrickson, 1983) or natal males (Ehardt & Bernstein, 1986), or change in the male hierarchy (Bernstein, 1968). Further, there is seasonal variation in the frequency of overthrows in captivity; they are more frequent in the breeding season, likely due to overall heightened aggression associated with mating competition (Eaton et al., 1981). Oates-O’Brien et al. (2010) suggests that the age of the alpha female may be of critical importance because older females are more experienced, implying that as females age and gain experience, they become less prone to insubordinate aggression or can suppress it more effectively.

1.4 Practical Applications

The results of this study have two types of broader significance: one practical and one evolutionary. Here we review the practical implications of this study, pertaining to the management of rhesus macaque populations, particularly in captivity.

Captive Breeding Groups

Many thousands of rhesus macaques are maintained in captivity all over the world. Although there are considerable numbers in zoos and sanctuaries, the biggest captive pool is maintained for biomedical research. In 2010, there were 71,317 non-human primates maintained for research in the United States, the majority of which were macaques (Animal and Plant Inspection Service, 2010). Rhesus macaques are commonly used in biomedical research due to their robustness in captivity, genetic similarity to humans, and abundance in the wild. In captivity, group housing most closely simulates the social environment natural to macaques, and is beneficial for their fecundity and psychological well-being (Novak & Suomi, 1988; Olsson & Westlund, 2007). Therefore captive breeding programs like those at National Primate Research Centers in the United States commonly house rhesus macaque breeding colonies in large (20-200) multi-male, multi-female groups. These groups exhibit heightened rates of aggression and trauma compared to wild groups (Thierry et al., 2004). Social overthrows are relatively common in captive groups, and typically result in serious injury or death to many group members, as well as subsequent disbanding of the group. Managers of captive rhesus macaque groups seek new methods for ameliorating deleterious aggression and social instability. Because social overthrows are a consequence of extreme insubordinate aggression, understanding risk factors for such aggression could facilitate prevention and prediction of social overthrows.

Wild Populations

Like other modern pest species, macaque species are successful in part because they are able to live commensally with humans and exploit the resources that are provided by humans (e.g., waste, agriculture) (Gumert, 2011). Rhesus macaques have thrived alongside humans for thousands of years. However, even they aren't immune to the pressures of human activity and have undergone radical population fluctuations in the past century. For example, in the 1960s and 1970s, rhesus populations in India declined by 80 to 90 percent due to habitat destruction, overharvesting for export to laboratories and culling prompted by crop-raiding (Southwick et al., 1983). After protections were instated, rhesus populations in India rose again to the point of problematic overabundance. This has resulted in increased human-monkey conflict, including crop destruction and disease transference (Paterson & Wallace, 2005). These problems illustrate the need for active management of rhesus populations, especially since conflict is likely to be continually exacerbated by increasingly crowded human populations. Management of wild populations may include capture and containment, either temporarily (e.g. for sterilization/translocation) or permanently, especially in India where culling is not legally or culturally permissible. Thus management of wild populations will often necessitate a captive component, which can be facilitated by knowledge of rhesus behavior and patterns of deleterious aggression.

CHAPTER 2: Dyadic age and rank dynamics and social support influence the likelihood of insubordinate aggression among female rhesus macaques (*Macaca mulatta*)

2.1 Introduction

Stability in biological systems is defined as the persistence of regularities over time (Krakauer, 2006). Social systems represent a balance between stability and change. Many social species form stable groups where membership is consistent over time. This social stability can be advantageous because it allows increased predictability in social interactions, improved behavioral coordination, and role partitioning. However, individuals and groups must also be able to respond to changing environmental and individual conditions; therefore, social systems must be capable of changing over time. Thus animal societies are complex, dynamic systems that may be in constant flux as individuals and communities gauge their options and interests, and pattern their behavior and relationships within the context of their social and physical environment.

Hierarchical structuring of dominance relationships is a common organizing principle among gregarious species that improves the average fitness of group members and increases group stability through reducing conflict and disorder (Wilson, 1975; Jones, 1981; Moosa & Ud-Dean, 2011). Although group characteristics and network structure are generated by the behavior and interactions of all individual group-members, hierarchical organization is generated by subordinate behavior. Submission, not aggression, is the essential signal that confirms the directionality of a dominance relationship. It is therefore subordinate animals that, through their deferential behavior, allow the establishment and persistence of social dominance hierarchies (Rowell, 1974). Similarly, hierarchical restructuring must be initiated by subordinate animals as they assert themselves over dominants or assume a dominant role left vacant through morbidity or mortality. Subordinates may act alone or in coalitions, and their challenge often necessitates aggression towards the dominant animal (de Waal, 1977; Holekamp & Smale, 1991). In the rigid, despotic societies of rhesus macaques, existing social order is vigorously reinforced with often intense—and potentially injurious—aggression (Thierry et al., 2004a). Animals that attempt to increase rank are thus typically faced with strong aggressive resistance from dominants and often must engage in violent conflicts in order to gain rank. The consequences of losing these fights can be severe: individuals and even whole families are sometimes killed in the aftermath of large-scale overthrows (Beisner at al., 2011; McCowan et al., 2008; Oates-O'Brien et al., 2010).

Because it is costly to be low-ranking (Harcourt, 1987; Silk, 2002; Van Schaik & Van Noordwijk, 1988), low-ranking animals stand to benefit from increasing rank, and thus are expected to keep apprised of opportunities for social advancement within their groups. If the relative competitive abilities between animals or subgroups shift such that the lower-ranking animal or subgroup can outcompete higher-ranking animals, a challenge may occur.

It should be noted that rank challenge is one of many potential drivers of contra-hierarchical aggression. Conflicts may arise for a variety of reasons, and sometimes subordinates may be willing to fight dominants in order to achieve objectives other than rank acquisition, such as defense of kin or resources. However, it is likely that characteristics that influence individual rates of contra-hierarchical aggression do so across multiple contexts, including resource acquisition, self and kin defense, and rank contention. Among rhesus macaques, aggression towards dominant animals is inherently provocative in any context and therefore carries risk of conflict escalation. Potential costs of intense conflicts include morbidity, mortality, degradation of social relationships, increased receipt of aggression and exclusion from access to resources. These potential costs are likely weighed against estimated benefits of achieving an objective (e.g. securing a resource, gaining rank, protecting offspring, avoidance of bodily harm), taking into account predicted likelihood of success.

Thus, female rhesus macaques are expected to 1) collect information about their relative competitive ability and potential opportunity to obtain an objective; 2) assess the potential benefits of gaining their objective; 3) assess the risk of challenging dominant animals; and 4) take action to gain their objective when there is opportunity and relatively low risk relative to potential gains.

Factors Affecting Competitive Ability

In macaques, competitive ability and rank acquisition are affected by both individual attributes and social support (Chapais, 1988; Datta, 1983, 1988; Datta & Beauchamp, 1991) . Individual attributes that may contribute to competitive fitness include physical size, age, strength and intelligence as well as personality characteristics such as boldness, reactiveness, and tolerance (McCowan et al., 2011). An animal's competitive ability is also affected by their access to social support, particularly in aggressive contexts. In rhesus, this support is most reliably provided by maternal kin, but may also be provided by unrelated allies of either sex within the group (Chapais, 1992, 1995). Therefore having a large, supportive matriline and many strong extra-matriline social bonds may improve an individual's competitive ability through increasing aggressive aid. And since a female's mother is perhaps her most reliable ally in fights, a mother's absence may reduce her daughters' competitive ability (de Waal & Luttrell, 1986).

Assessing Opponent Competitive Ability

Information about relative competitive ability may be acquired by direct interaction or observation. Animals assess their relationships with both dominant and subordinate group members, and frequently engage in negotiating or maintaining status in those relationships (de Waal, 1986b). Macaques communicate about their dominance relationships using formalized submission signals such as ‘silent bared-teeth displays’; ‘rump presents’, wherein animals stand erect and motionless with their rumps oriented away from dominants; and ‘displacements’, wherein subordinates move away from dominants without any aggressive provocation (de Waal & Luttrell, 1985; Hausfater & Takacs, 1987; Maestripieri & Wallen, 1997; McCowan et al., 2008). Aggression or intimidation by dominants often forces subordinates to offer formalized submission in exchange for peaceful coexistence, allowing them to avoid escalating conflict that, precedent suggests, they are unlikely to win. Animals may solicit signals of submission or subordination to confirm or reinforce dominance (de Waal, 1986b; McCowan et al., 2008; Thierry et al., 2004). Alternatively, individuals may reinforce their dominance by disrupting the grooming bouts (Chapais, 1992) or matings (Niemeyer & Anderson, 1983) of lower-ranking animals. The subordinate’s response—and the response of her allies—to such provocations can provide information about her attitude and competitive ability, and/or the strength of her alliances. In turn, subordinates may vary their degree of submissiveness in both aggressive and non-aggressive contexts and gain information about the dominant’s competitive ability, alliances or level of tolerance.

Taking Action: Contra-Hierarchical Aggression

In primate species characterized by strong, stable dominance hierarchies, contra-hierarchical aggression usually occurs in less than 5% of observations (Missakian, 1972; Silk et al., 1981) compared to a rate as high as 15% in species characterized by weak or unstable hierarchies (Isbell & Young, 2002). The observation of contra-hierarchical aggression requires a previously described dominance hierarchy. After the relative ranks of individuals in a group have been assessed, then aggression that is directed from a lower-ranking animal to a higher-ranking animal can be considered contra-hierarchical. However, there are several considerations to be made when evaluating dominance relationships. Firstly, it is possible for rank relationships to be undecided; in these cases, bi-directional aggression would not be contra-hierarchical; instead, it would reflect an unresolved dominance relationship. Secondly, observed instances of contra-hierarchical aggression may reflect normal shifting in rank relationships. For example, young animals may not be able to individually outrank older individuals without aggressive support from their mothers; as they mature, however, they may assert themselves and assume their inherited rank (Datta, 1988). Bi-directional aggression resulting from ambiguous rank or the process of ascending to rightful rank is different from contra-hierarchical aggression that occurs between animals that have well-established dominance relationships. In the latter case, contra-hierarchical aggression may be thought of as “insubordinate aggression”. Insubordinate aggression may represent either protest (in which the subordinate is contesting the actions, but not the dominance, of the dominant animal) or true challenge (in which the subordinate is contesting the direction of the dominance relationship). Since it is difficult to assess the intent of an insubordinate animal, except in rare observations of protracted bouts of severe bidirectional aggression, this work will not address those differences; instead we propose that insofar as insubordinate aggression reflects willingness to challenge higher ranking animals, it may be an important indicator of hierarchical instability within a dyad or a group. Both McCowan et al. (2008) and Beisner et al. (2011) showed that redundancy and non-ambiguity in dominance relationships is positively associated with group stability among rhesus macaques, which supports the assumed link between insubordinate aggression on the dyadic level and instability on the group level.

We hypothesized that among female dyads with well-established dominance relationships, the likelihood of insubordinate aggression is influenced by attributes of both opponents, including age, weight, rank, and availability of social support.

Predictions

P1) Insubordinate aggression will be more likely among dyads close in weight or rank, and less likely among dyads with high disparity in weight or rank.

P2) Older subordinates will be more likely to be insubordinate than young subordinate females, whereas younger dominant females are more likely to receive insubordinate aggression than older dominant females.

P3) Increased social support available to subordinates, measured in number of female kin, grooming partners, and aggressive allies, will increase the likelihood of insubordinate aggression. Increased social support available to dominants, on the other hand, should decrease the likelihood of insubordinate aggression.

2.2 Methods

Study Site and Groups

This study was conducted at the California National Primate Research Center (CNPRC), in Davis, California, from June 2008 to April 2010. The study subjects were 357 adult female rhesus macaques ranging in age from 4-25 years old. The subjects were members of 6 mixed-sex social groups (groups 1, 5, 8, 10, and 18) housed separately in 0.2 ha corrals. The groups were each comprised of between 108-197 individuals. All groups were well established, having been freely breeding in captivity for greater than 10 years each, and had matrilineal social structure.

Two observers at a time cooperatively recorded most or all aggressive, submissive, and status interactions among group members using event-sampling design developed by Beisner et al. (2011). These events were characterized as an ordered series of dyadic transactions, initiated by one individual and directed toward a recipient, whose response or lack of response was recorded. Prolonged or polyadic interactions were recorded as a series of dyadic interactions, with no limit on the number of transactions occurring in a single event. Aggression and submission were classified according to level of severity; aggression was categorized into seven levels, and submission into five levels (Table 1).

Table 1. Levels of aggression and submission recorded for this study.

Level	Aggression	Submission*
1	Stare, brow flash, ear flap	Turn away
2	Vocal threat, threat + follow	Move away
3	Lunge, mild slap or push	Run away short <3m
4	Short chase <3m	Run away long >3m
5	Long chase >3m	Crouch
6	Bite	
7	Bite >5 seconds	

*Silent bared-teeth displays were recorded if they occurred during submission.

Peaceful signals of subordination (status signals) were recorded during periods of low conflict (Flack et al., 2006; McCowan et al., 2008). These included silent bared-teeth displays, rump presents, and displacements observed in peaceful contexts. Grooming was recorded during affiliation scans conducted every 30 minutes. Affiliation scans were aborted if conflict erupted during a scan.

Groups were observed for 6 hours per day for 4 days per week for 10 weeks each, with an average of 193 hours of observation per group (Table 2). Data was collected between June 2008 and April 2010 by four observers (BAB, MEJ, ANC, SKS). Inter-observer reliabilities were above 85 percent.

Table 2. Attributes of groups and data collected.

Group	Average Group Size	Adult Females in Group	Female Dyads Observed in Conflict	Observation Hours
1	178	51	459	182
5	137	59	993	211
8	157	76	1484	209
10	165	68	773	178
14	108	38	547	203
18	197	65	498	176

Data Analysis

Assessing Non-Ambiguity in Dominance Relationships

Aggressive interactions among females ≥4 years old were selected for analysis. Only dyads whose dominance relationships were shown to be strong and certain were considered. This was determined through assessing the direction, frequency, and decisiveness of conflicts among female dyads. Additionally, a social network approach was used to supplement direct observations of dominance interactions, by filling in missing cells of the win/loss matrix using indirect dominance pathways from the dominance network (Fushing et al., 2011).

Among rhesus macaques, information about dominance relationships can be obtained through observation of aggressive interactions and status signaling. There is heterogeneity in both the degree to which one animal is dominant to another, and the availability of information about a dominance relationship. Both factors contribute to degree of ambiguity in dominance relationships, from an outside perspective.

Dominance Probability

Lack of direct information about a particular dyad is usually due to insufficient sampling and/or low frequency of interaction. This type of uncertainty can exist alongside real ambiguity, which instead results from conflicting evidence about the direction of dominance. Informational deficits exist because in large groups, many animals are rarely or never observed to interact. Dyads never observed to engage in direct dominance interactions might nonetheless have a mutually understood dominance relationship; on the other hand, they might have a contested or nonexistent dominance relationship. For dyads that have few direct interactions, a network approach can be useful in generating predictions about the strength and direction of dominance relationships. This is because linear and corporative hierarchies are usually characterized by transitivity (Fushing, 2011). That is, the dominance relationship between two animals can be inferred by their mutual relationships with a third party. For example, if i is dominant to j, and j is dominant to k, it is likely that i is also dominant to k. The more numerous and unequivocal these indirect links are, the more certain the dominance inference becomes. Thus, even if two animals are never observed to interact, strong predictions may be made about their dominance relationship if have numerous and consistent indirect connections.

To estimate direction and ambiguity of pairwise dominance relationships, and generate an estimated linear dominance hierarchy, dominance probability (DP) scores were calculated for all dyads using a network generated from decisive aggressive interactions (aggression met with submission) using the percolation and conductance method described in Fushing et al. (2011). Both direct links and transitive paths between each pair in the network were used to determine the probability that one outranked the other during the data collection period. A strong direct unidirectional link between two individuals was reinforced by supportive transitive relationships.

DP scores near 1.0 indicate that there are an abundance of direct and/or transitive paths in the network of decisive wins that confirm the directionality of a pair's dominance relationship. On the other hand, DP scores near 0.5 indicate either evidence of direct conflict over rank (e.g. a large amount of bidirectional aggression), lack of direct or transitive links, or a combination of these factors. DP scores were used for two purposes in this study: 1) to provide information about the direction and certainty of dyadic dominance relationships and 2) to generate a linear hierarchy for all adult females in each group using a matrix approach.

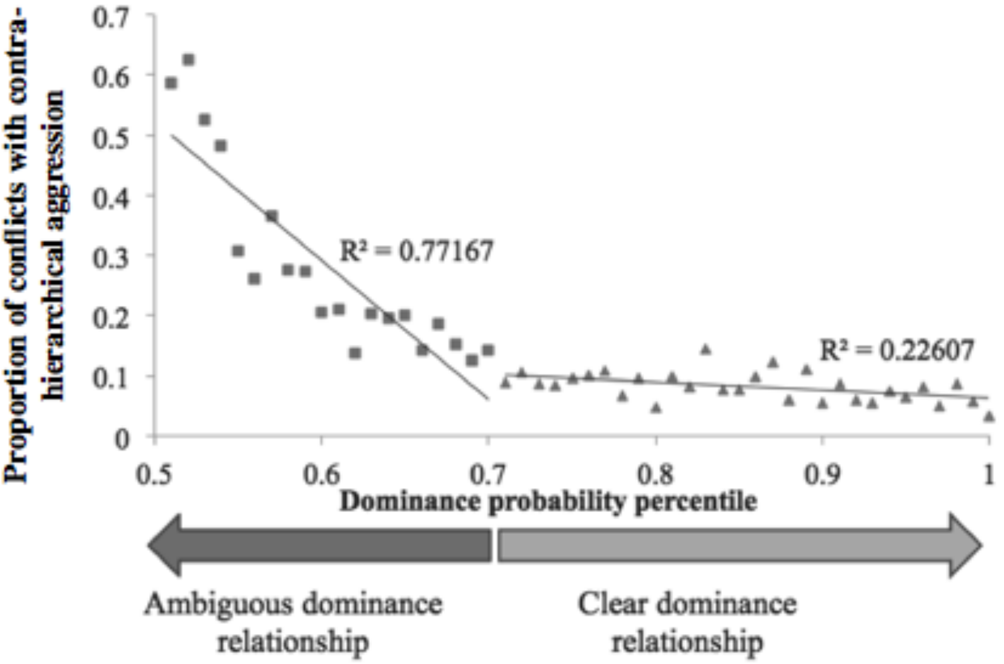
Rate of Contra-Hierarchical Aggression

To identify contra-hierarchical aggression, the direction of dominance within dyads must first be estimated. Dominance probabilities were used to estimate the likely direction of dominance. Dyads with DPs equal to 0.5, indicating complete uncertainty about the direction of dominance, were dropped from the analysis, because assessment of contra-hierarchical aggression requires some dominance asymmetry. For the remaining dyads with DPs $\neq 0.5$, one animal was distinguished as likely dominant to the other. From the set of animals with a discernable dominance relationship, we attempted to identify and exclude those dyads with shifting or ambiguous rank relationships.

To do this, rates of contra-hierarchical aggression were calculated for each dyad. The per-dyad rate of contra-hierarchical aggression was the proportion of each dyad's total conflicts wherein aggression was directed towards the animal identified as dominant. To assess the relationship between contra-hierarchical aggression and dominance certainty, this rate of contra-hierarchical aggression was plotted against DP score.

Figure 1 illustrates that the rate of contra-hierarchical aggression among dyads sharply declines as dyadic DP increases from 0.5 to 0.7. However, over DP = 0.7, there is little relationship between increasing DP and rate of contra-hierarchical aggression. Thus, DP scores seem to have validity in distinguishing between clear and ambiguous dominance relationships, as reflected by rate of contra-hierarchical aggression. We infer that dyads with DP <0.7 may have shifting or ambiguous rank relationships, whereas dyads with DP >0.7 have clear dominance relationships. Since this study is concerned with investigating patterns of insubordinate aggression among animals with well-established dominance relationships, we excluded those dyads with DP <0.7.

Figure 1: Incidence of contra-hierarchical aggression sharply decreases with increasing dominance probability percentile, until 70% probability. Above 70% dominance probability, there is no relationship between dominance probability and contra-hierarchical aggression.



Other Excluded Dyads

As an additional measure to ensure that only dyads with strong dominance relationships were considered, Bayesian hierarchies were generated based on status signaling using WinBUGS software, version 1.4.3 (Lunn et al., 2000). Rankings based on status signaling should correspond with rankings based on aggression, so contradictions between the two types of hierarchies might be indicative of uncertainty in the dominance relationship. Therefore, only dyads whose dominance relationship was affirmed by both aggression-based DP matrices and Bayesian status-signaling hierarchies were included in the analysis.

Finally, intra-matriline dyads were excluded because intra-matriline rank relationships and aggression may be different than relationships between females of different matrilines, and because one of the predictors tested, matriline size, only has validity in inter-matriline conflicts.

Statistical Analysis

Out of 11,951 records containing aggression within female dyads fitting the criteria described above, there were 967 observations of insubordinate aggression, wherein the subordinate animal directed aggression towards the dominant animal. Our aim was to compare aggressive interactions wherein insubordinate aggression occurred (N=967) to those without insubordinate aggression (N=10,984), in order to identify attributes of conflict opponents that might be associated with risk of insubordinate aggression. To identify such predictors of insubordinate aggression, the data were fit to a linear mixed-effects model with a binomial outcome (insubordinate aggression occurs, yes/no). Random effects were included for group (n=6), dominant animal identity (n=299) and subordinate animal identity (n=313). Fixed effects included age (age of dominant, age of subordinate, and age difference); weight (weight of dominant, weight of subordinate, and weight difference), rank (rank of dominant, rank of subordinate, and rank difference), presence of the subject's mother in the group (for dominant and for subordinate, yes/no), matriline size as expressed by proportion of the group belonging to an animal's matriline (for dominant and subordinate), and Shannon diversity indices for each individual's pool of groomers and aggressive allies, as well as interactions between these variables (Table 3). The Shannon diversity index was used to quantify the social support (affiliative and aggressive) available to the subject. The measure reflects both the amount of social support given to the subject and the diversity of social partners. Shannon's diversity index (H) is measured by first counting the total number of social interactions of interest (S) for each subject, then determining the proportion of S that is contributed by the subject's *i*th social partner (p_i). Then H for each subject is the negative sum of p_i multiplied by the natural log of p_i, or

$$H = -\sum_{i=1}^{S} p_i \ln p_i$$

For the diversity index of grooming received (H_G), S_G was the total number of observations of the subject receiving grooming, and p_i was the proportion of S_G given by the *i*th grooming partner. For the diversity index of aggressive support received (H_A), S_A was the total number of instances in which the subject received aggressive support, and p_i was the proportion of S_A contributed by the *i*th ally. Animals were considered co-aggressors with the subject when they (1) intervened in fights in support of the subject, or (2) simultaneously aggressed other animals in coalition with the subject.

Table 3. Description of model parameters.

	Description
Data	Observations of conflicts (n=11591) between adult females with well established dominance relationships. A conflict was defined as an event in which at least one animal directed aggression towards the other animal.
Outcome: Insubordination	Insubordination was defined as aggression directed from the subordinate to the dominant animal in any context, regardless of the dominant's response.
Group (random effect)	A random effect was included for the social group to which the subjects belonged (n=6).
Dominant identity (random effect)	A random effect was included for the identity of the dominant animal in each dyadic event (n=299).
Subordinate identity (random effect)	A random effect was included for the identity of the subordinate animal in each dyadic event (n=313).
Age*	Age of each subject in years.
Presence of mother*	Whether or not the subject's mother was present in the cage for >50% of the study period.
Weight Difference	Dominant animal's weight minus subordinate animal's weight.
Rank*	Rank of the dominant animal within the female dominance hierarchy (highest rank = 1) divided by the lowest (maximum) possible rank to control for differences in group size.
Rank Disparity	Relative difference between the ranks of the dyad. Animals were assigned sequential ranks, with 1 being the highest ranking, using DP matrices. Rank disparity was subordinate minus dominant rank divided by the maximum rank for each group, to control for group size.
Matriline Size*	Proportion of animals in the group belonging to the subject's matriline. Males over 4 were not included as part of their mother's matriline.
Groom Diversity Index*	Shannon entropic measure for the diversity of animals that groomed each subject. The measure reflects the frequency of grooming received and the diversity of groomers. Groom diversity index was calculated using $H = -\sum_{i=1}^{s} p_i \ln p_i$ where p_i is the proportion of total observed grooming (S) received from the *i*th groomer.
Ally Diversity Index*	Shannon entropic measure for the diversity of each subject's co-aggressors (partners in aggression). The measure reflects both the amount of aggressive aid given to the subject, and the diversity of its partners in aggression. Ally diversity index was calculated using $H = -\sum_{i=1}^{s} p_i \ln p_i$ where p_i is the proportion of total observed instances of aggressive support received by the subject (S) given by the *i*th ally.
Matriline Relatedness*	Average genetic relatedness among the members of the subject's matriline. Genetic relatedness was calculated for all maternally related dyads using pedigree information, then averaged by matriline.
*Measure was calculated and included as a separate variable for both the dominant and subordinate opponent.	

Using R (version 3.0.2), we ran a series of models including many possible combinations of the above variables, starting with the simplest models and adding variables (R Core Team, 2013). We used Akaike's Information Criteria (AIC) scores to determine the best-fit model. Models were considered equivalent if their AIC scores differed by less than 2 (Burnham & Anderson, 2002).

2.3 Results

We selected and analyzed 11,951 records containing aggression between females with non-ambiguous dominance relationships. Nine hundred and sixty-seven of these records contained observations of contra-hierarchical aggression, which we consider to be instances of true insubordinate aggression because they occurred despite robust dominance relationships. Thus we report an overall insubordination rate of 8.1%, which is higher than previously reported rates of approximately 5% among captive bonnet macaques (*Macaca radiata*) (Silk et al., 1981) and free-ranging rhesus (Missakian, 1972).

We fit a linear mixed-effects model to a binary outcome—the occurrence of insubordinate aggression—using a variety of predictors. The most parsimonious best-fit model included fixed effects for: (1) the age of the dominant animal, (2) the age of the subordinate animal, (3) the dyad's weight difference (dominant weight minus subordinate weight), (4) the dyad's rank disparity, (5) the subordinate animal's diversity of aggressive allies, (6) the subordinate animal's diversity of groomers, (7) the subordinate animal's matriline size, (8) an interaction between the age of the dominant animal and the subordinate animal, and (9) an interaction between the subordinate's age and the dyad's rank disparity (Table 3).

Table 3. Best-fit model

Outcome = insubordinate aggression occurs (yes/no)

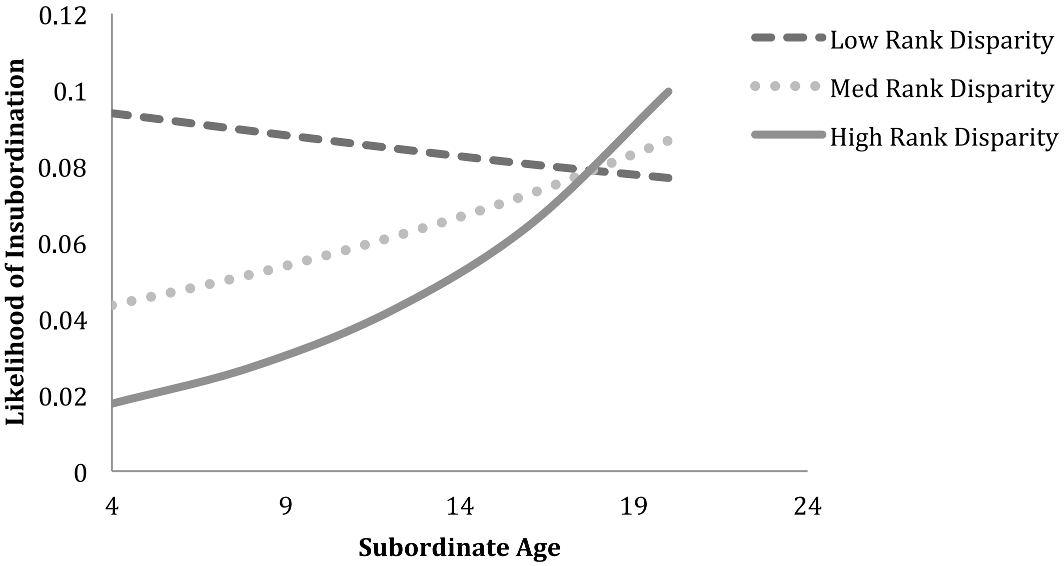
	b*	p	
(Intercept)	-2.751	0.000	***
Weight Difference	-0.128	0.000	***
Age of Dominant	0.014	0.527	
Age of Subordinate	0.023	0.373	
Rank disparity (relative)	-3.311	0.000	***
Subordinate's Ally Diversity	0.391	0.001	***
Subordinate's Groom Diversity	0.077	0.024	*
Subordinate's Matriline Size (relative)	-3.020	0.002	**
Interaction terms:			
Age of Dominant*Age of Subordinate	-0.006	0.004	**
Age of Subordinate*Rank Disparity	0.186	0.000	***

*b values are on a log-odds scale

Rank Disparity

An interaction between rank disparity and the age of the subordinate opponent affects the likelihood of insubordinate aggression (β=0.186, p=<0.000) (Figure 2). For young subordinate females, likelihood of insubordinate aggression is strongly mediated by the degree to which they are outranked by their opponent. However, the inhibitory effect of high rank disparity declines as subordinate animals age. For elderly adult females, high rank disparity does not inhibit insubordinate aggression. That is, older females do not seem to modulate their aggressive behavior based on the degree to which they are outranked by their opponent.

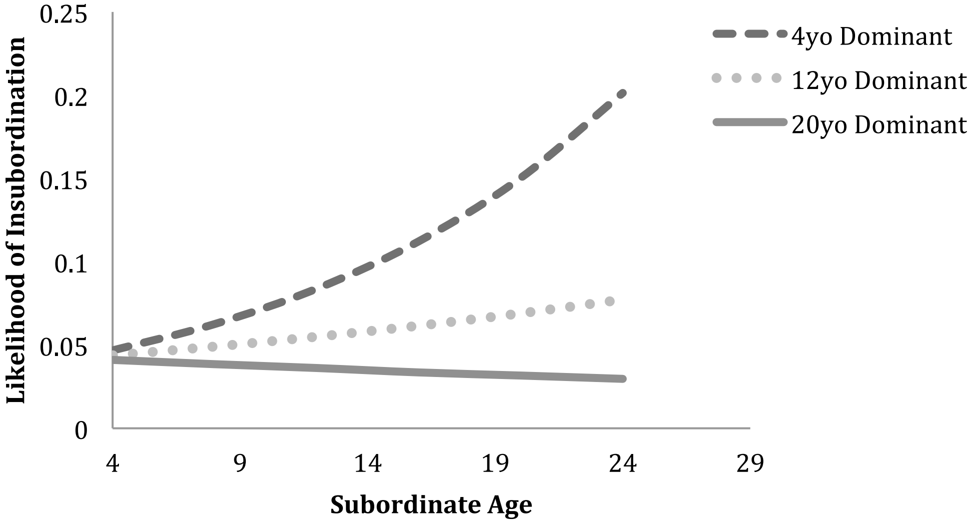
Figure 2. High rank disparity reduces the likelihood of insubordinate aggression, but the effect of rank disparity diminishes as subordinate females age. Rank disparity does not suppress insubordinate aggression among senior females (>18 years old).



Age Difference

The likelihood of insubordinate aggression is affected by dyadic age dynamics (β=-0.006, $p<0.01$) (Figure 3). Young subordinate females are predicted to have low likelihood of insubordinate aggression, regardless of their opponent's age. As subordinate females age, they are increasingly likely to be insubordinate, but this effect is strongly mediated by the dominant opponent's age. The likelihood of insubordinate aggression increases with increasing subordinate age when the dominant opponent is young. However, when the dominant animal is very old, there is much less increase in insubordinate aggression with increasing subordinate age.

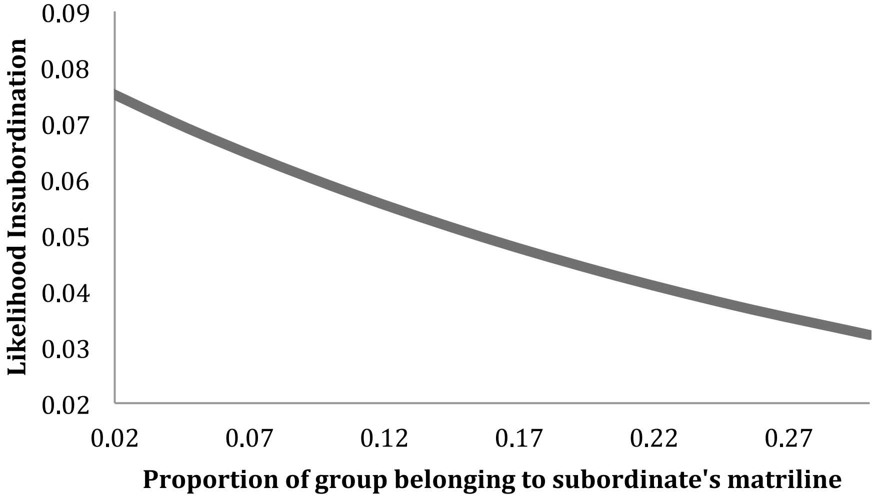
Figure 3. Dyadic age dynamics predict the likelihood of insubordinate aggression. Older females are more likely to be insubordinate, especially towards young dominants.



Subordinate Matriline Size

Contrary to our prediction, increasing matriline size, as measured by the proportion of the group belonging to the subordinate's matrilines, decreased the likelihood of insubordinate aggression (β=-3.020, p=<0.01) (Figure 4). Females belonging to small matrilines are more than twice as likely to be insubordinate than those belonging to large matrilines.

Figure 4. Likelihood of insubordinate aggression decreases with increasing subordinate matriline size (as measured by the proportion of the group belonging to the subordinate's matriline).



Social Support: Diversity of Groomers and Allies

As predicted, measures of the subordinate's access to social support within the group affected the likelihood of insubordinate aggression. We tested two diversity indices to reflect the frequency and diversity of partners in aggression (ally diversity) and affiliation (groom diversity). A subordinate who has frequent support in conflicts from a variety of different individuals is more likely to engage in insubordinate aggression than an individual who has little such support (Figure 5). Likewise, subordinates who receive frequent grooming from a variety of partners are also more likely to be insubordinate (Figure 6). Interestingly, social support of dominants was not predictive of their likelihood of receiving insubordinate aggression.

Figure 5. Subordinate females with high ally diversity indices (reflective of frequent aggressive support from many partners) are more likely to engage in insubordinate aggression than those with low ally diversity indices.

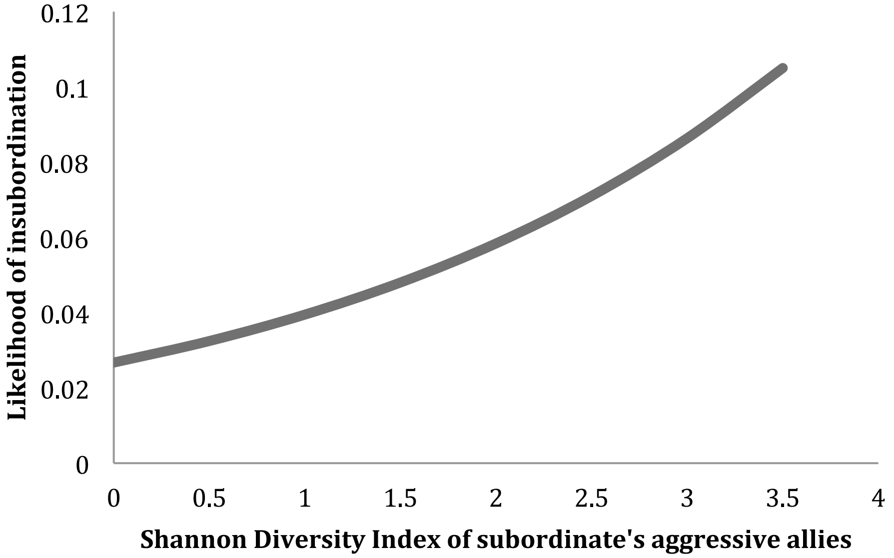
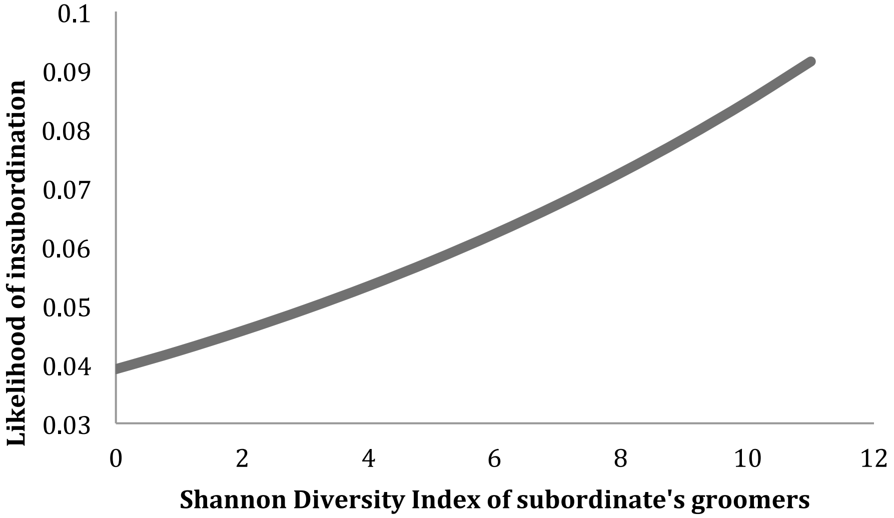


Figure 6. Subordinates who receive frequent grooming from a variety of partners are more likely to engage in insubordinate aggression than those that receive little grooming and/or have few grooming partners.



2.4 Discussion

Age Dynamics and Rank Disparity

The result that age dynamics predict the likelihood of insubordinate aggression, even when weight and rank disparity are held constant (Figure 3), suggests that the age relationship of female opponents has either a direct effect on insubordinate aggression, or an indirect effect through non-physical correlates of age (such as increased experience or social support resulting from long tenure in the group). Weight is a correlate of age that has been shown to affect patterns of aggression and dominance in many animal species (Parker, 1974), and body size and age are correlated with rank for both male and female macaques (Small, 1981; Sprague, 1998). However, it is well documented that, for most social primate species, rank and power are not determined simply through physical contests (Hrdy & Hrdy, 1976; Sade, 1967; Missakian, 1972; McCowan, 2011).

These results support that contests among female rhesus involve complex power dynamics, wherein age is an important factor independent from body size. In general, young dominant females appear to be more vulnerable to insubordinate aggression, especially in conflicts with older females. In contrast, older females are less vulnerable to insubordinate aggression, especially from young females. Young subordinate females show low rates of insubordinate aggression, regardless of opponent age. Conversely, older subordinate females appear to modulate their insubordinate behavior according to their opponent's age.

Thus young and old females appear differentially sensitive to their opponent's age. The finding that young females are generally unlikely to be insubordinate regardless of opponent age may be linked to the process of young adult females solidifying their 'basic' rank, or the rank that they are able to defend independently (Kawai, 1965), as described by Datta (1988). As young female macaques mature, they may have to overcome a large discrepancy between their 'dependent' rank (i.e. the rank they assume with the support of others, particularly their mother), and their 'basic' rank, which is the rank they can independently defend (Kawai, 1965). The target rank has been referred to as 'genealogical' rank, usually the rank just below the mother (Chapais, 1988; de Waal, 1977). While in the process of assuming her 'basic', 'genealogical' rank, a female may be less secure in her social position and therefore less likely to challenge higher-ranking animals. Of course, such females would still be expected to challenge those that outrank them in basic but not genealogical rank, as part of the process of rank ascension.

Older subordinate females appear not to modulate their insubordinate behavior according to degree of rank disparity between themselves and their opponent (Figure 2). While rank disparity has an inhibitory effect on younger subordinates, it appears to have little effect on older subordinates. Like the interaction between dominant and subordinate age, we observe differential responsiveness to opponent characteristics according to subordinate age. In this case, it is younger females who show sensitivity to rank difference, changing their degree of deference to dominants based on the degree to which they are outranked. Again, we find that young females are generally less likely to be insubordinate than older females. One seeming exception that emerged in the present study was that young females are slightly more likely than average to be insubordinate to females close to them in rank. As with the previous result, this could also be associated with rank ascension in young females. Within the set of female dyads with non-ambiguous dominance relationships, there is likely a subset of young females who are in the process of rank ascension, challenging those females who outrank them in 'basic', but not 'genealogical' rank. This could result in the observed high insubordination rate for the subset of dyads in which rank disparity is low and the subordinate is young.

Old subordinate females, on the other hand, challenge dominants at a similar rate regardless of the degree to which they are outranked. This result may reflect that in matriarchal societies, social roles change as females age (Nakamichi, 1984), with older females increasingly adopting leadership roles within their matriline or group. Numbers of offspring or descendants were not significant predictors of insubordinate aggression in the model, so it does not appear that the observed age-related loss of inhibition is simply a result of increased need for progeny defense.

Considering both interactions—dominant age by subordinate age, and subordinate age by rank disparity—we find that overall, subordinate females of different ages respond differently to their opponent's characteristics. In particular, we find that old subordinates alter their level of insubordinate aggression based on their opponent's age, but don't respond differently to opponents based on rank disparity—old females are most likely to be insubordinate, and do so at similar rates when facing either females close or far from them in rank. Conversely, young subordinate females don't respond differently based on opponent age—they show low rates of insubordination regardless of their opponent's age. On the other hand, they do respond differently based on the degree to which they are outranked, and are much less likely to be insubordinate to much higher ranking females than those close in rank.

Social Capital: Access to Social Support

Our results show that a subordinate's access to social support, both aggressive and affiliative, affect her likelihood of insubordinate aggression. The finding that, for subordinate females, receiving frequent aggressive support from many different individuals increases the likelihood of insubordination could have several non-mutually exclusive explanations. These include: (1) subordinate females might be emboldened by the perception that other animals will provide support if conflict escalates, or (2) dominant females might be more tolerant of well-connected subordinates because such subordinates might receive aggressive aid if conflict escalates. Alternatively, attributes of subordinate animals that are associated with extensive networks of aggressive support (e.g. social power, personality) may also associated with either (1) the tendency to be insubordinate, or (2) more permissive treatment of such subordinates by dominant animals. Finally, there is a possibility that having many aggressive alliances promotes insubordinate aggression through reciprocity or biological markets. Reciprocity of agonistic aid, in which animals are more likely to aggressively support others that have done so for them in the past, is seen in many primate species, including macaques (de Waal & Luttrell, 1988). As a result, animals that receive much aggressive support from many allies may be more likely to intervene in fights to support those allies. Biological market theory provides a framework for understanding such reciprocity in cooperative and altruistic behavior (Barrett & Henzi, 2006;

Noë & Hammerstein, 1994). Within this framework, agonistic aid represents a commodity which can be traded in kind, or for other commodities such as grooming (Barrett et al., 1999).

The result that increasing affiliative support increases a subordinate's likelihood of insubordinate aggression might have somewhat different explanations than those suggested for aggressive support because there is no direct link between a female's affiliative relationships and her likelihood of receiving support during conflicts. Although it seems plausible that being socially well connected might result in increased access to both affiliative and aggressive support, the measures for grooming partner diversity and aggressive ally diversity were not positively correlated (Pearson's r = 0.192). Therefore, there is no reason to expect that subordinate females with high levels of affiliative support should either (1) be emboldened during conflicts or (2) receive more permissive treatment from dominant animals due to the perception of availability of aggressive support. However, characteristics that promote high diversity of grooming partners may also promote insubordination, as with diversity of conflict allies. Also, it is again plausible that biological market theory can explain the relationship between grooming partner diversity and insubordination, because grooming may be exchanged for agonistic support (Schino, 2007). This could lead to correlation between number of grooming partners and the likelihood of participating in fights against higher-ranking animals, which could in turn affect likelihood of insubordinate aggression.

Social Capital: Matriline Size

The result that increasing matriline size was correlated with decreased insubordinate aggression (Figure 4) was unexpected. One possible explanation is that in the absence of kin support in fights, females may have to be more aggressive to defend their position. Another possible explanation for this observation is differential punishment of subordinate females by dominants, according to matriline size. Since members of a matriline often support each other in conflicts, matrilines often form aggressive coalitions during group conflicts (Bernstein & Ehardt, 1985). Therefore large matrilines may constitute a bigger threat to higher-ranking animals, and as a result dominant females might more actively suppress or punish insubordinate aggression from females with large matrilines, and conversely might be more permissive of females without much kin support.

A third hypothesis is that genetic fragmentation of matrilines, reflected by low matriline relatedness, reduces the likelihood of insubordination. Matriline relatedness is negatively correlated with matriline size (Pearson's r = -0.645). Matrilines with high genetic fragmentation have increased intra-matriline aggression, subgrouping in grooming networks, and greater wounding rates, suggesting an overall link between genetic fragmentation and stability at the matriline level (Beisner et al., 2011). For large, fragmented matrilines, matriline size could be uncoupled with availability of actual social support, and/or increased infighting within these matrilines could reduce likelihood of insubordinate aggression because (1) females may spend more time fighting with kin relative to small, close-knit matrilines, or (2) females from unstable matrilines may seek to garner support from higher ranking non-kin, and therefore may avoid provoking them through insubordinate aggression.

Finally, there is a possibility that small matrilines may be better able to ascend in rank than large matrilines because small matrilines tend to have higher cohesiveness, aiding coordination of rank ascension efforts at the matriline level (Beisner et al., 2011). If members of small matrilines are more effective in coordinating rank ascension efforts, they may be more likely to be insubordinate, relative to members of large matrilines.

Characteristics of Dominant Animals

We have found that in dyadic conflicts, many characteristics of the subordinate female predict the likelihood of insubordination. In contrast, most features of dominant animals did not emerge in the best-fit model and thus appear to be less predictive of insubordinate aggression. Counter to our predictions, neither the dominant's access to aggressive and affiliative support, nor her matriline size, appear to influence her receipt of insubordinate aggression. Dominant age and rank *per se* were not significant predictors. Dominant age was important as an interaction with subordinate age (young dominants were more likely to receive insubordinate aggression from older subordinates, see Figure 3) and dominant rank was significant only as rank disparity. This is interesting because it highlights the importance of the subordinate's characteristics as factors affecting the occurrence of insubordinate aggression, whereas features of dominant animals appear important only relative to the subordinate's features.

2.5 Conclusion

The results of this study suggest that characteristics of individuals, dyads, and groups can affect the likelihood of insubordinate aggression at the dyadic level. We propose that examination of patterns of insubordination at the dyadic level can provide insight into group-level stability. Group stability is maintained despite conflict between individuals and thus conflict management behavior constitutes a critical stabilizing force for social groups. For primates and many other animals, dominance hierarchies are an important conflict reduction mechanism. For species characterized by high levels of intra-group aggression such as rhesus macaques, rigid dominance hierarchies are strictly maintained, rank change is generally suppressed, and deterioration or reversal in rank relationships is often dangerous for individuals and for groups, and sometimes resultant in social collapse. In such societies insubordinate aggression is undoubtedly linked to group stability, since social overthrows represent an extreme degree of insubordinate aggression. However, closer examination might reveal a more nuanced relationship between insubordinate aggression and group stability in hierarchical societies. Insubordinate aggression represents an avenue through which subordinate females can negotiate power and circumstance in their relationships with dominant animals, and there is likely a level of insubordinate aggression that is compatible with and even supportive of stability. It is not clear what this optimal level is, or in general how rates of insubordination correlate with overall group stability.

What is clear is that group social structure is maintained and organized by the actions of individuals, and characteristics of individuals importantly affect the interactions that generate group-level attributes. Animals in subordinate roles are the agents that, through insubordinate aggression to dominants, initiate hierarchical upheaval. Therefore the behavior of individual females towards dominants can either support or destroy group stability. While the behavior of dominants probably affects stability also, it does so in a less proximate way. This study supports the importance of subordinate behavior by showing that attributes of females in subordinate roles, such as age and social capital, are more important determinants of an insubordinate event than the corresponding attributes of the dominant animal.

Further, this study reveals that, despite a rigid and despotic social environment, rhesus macaques do not passively inherit and accept their societal status, but rather are dynamic agents who appear to consistently monitor and test the relationships that structure and limit their social opportunities, and integrate complex information to determine whether to defer to or rebel against the impositions of dominant group members. Thus subordinate decision-making during conflicts, apparently based on attributes of self and opponent relevant to competitive ability and social support, may be a critical mechanism by which social order is either maintained or rejected in rhesus societies. Other research has highlighted the importance of other key stabilizing roles in primate groups, such as policers and individuals with high rank and social power (Flack et al., 2006; McCowan et al., 2011). The results of this study suggest that even low-ranking subordinates can be critical players whose behavior patterns may be usefully assessed in the study of robustness in hierarchical societies.

In particular, the present study suggests that 1) young alpha females might be vulnerable to overthrow if there are old, socially supported females in their group; 2) small, cohesive, closely related matrilines might pose a greater threat of overthrow than larger matrilines; 3) females who have high social support in both affiliative and aggressive contexts may constitute a threat to social stability even if they are low-ranking; 4) multiple risk factors may combine to produce a high likelihood of insubordinate aggression/overthrow (for example, if the highest ranking matriline has a young alpha female and there is a cohesive, well-socially supported matriline with elder members in the group). These results point to strategies for identifying individuals and groups at high risk of insubordinate aggression. This information could be useful in assessing stability and addressing problems with social aggression and overthrows in rhesus groups, especially in captive colonies. However, effects on group stability should be specifically addressed through analysis of whether high rates of insubordinate aggression at the group level are associated with high rates of conflict and wounding, or likelihood of social upheaval and collapse.

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