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# The Affiliative Social Relations Of Free-Ranging Rhesus Macaques In The Context Of Instability

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# The Affiliative Social Relations Of Free-Ranging Rhesus Macaques In The Context Of Instability

## Abstract

Across primates, socially integrated individuals exhibit improved genetic fitness compared to their peripheral conspecifics. However, the mechanisms through which this disparity operates is unclear. One hypothesis is that social bonds mitigate the stressors imparted by environmental instability. To date, this relationship has gone critically unexamined, owing to the inability to anticipate and account for instability in prospective research design. In this dissertation, I evaluate this hypothesis within a population of free-ranging rhesus macaques (*M. mulatta*). I employ a long-term behavioral data set comprised of 691 unique individuals across 6 groups, followed from 1 to 8 years. I employ the tool-kit of social network analysis to integrate social phenotypes at the individual, dyadic, and group-level. I examine two destabilizing events. First, I examine how affiliation patterns precede a matrilineal overthrow, an outburst of aggression which resulted in group dissolution. As a prelude to this analysis, I investigate the manifestation of rank instability more generally, and, in concert with other dimensions of social life, examine its relationship to psychosocial stress. Second, I examine affiliation in the wake of environmental disaster: here, that of Hurricane Maria, which in 2017 had caused near-complete deforestation. I find that instability leaves an enduring signature in expressions of psychosocial stress. In the context of instability, monkeys show critical transformations in their affiliative patterns — in frequency, variability, and direction — but in ways highly dependent on the type of instability experienced. Such transformations are not experienced uniformly across social units, but instead are concentrated upon those most likely to suffer (or endure) the costs of that instability. This analysis indicates that rhesus monkeys exhibit considerable social flexibility in response to environmental instability and that social bonds, rather than static, are continually renegotiated. Destabilizing events are rare but can impart instantaneously brutal fitness consequences. It is critical, then, that we accumulate case studies of their effects — messy though they may be — to avoid blind spots in our understanding of the evolution of social bonds.

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THE AFFILIATIVE SOCIAL RELATIONS OF FREE-RANGING RHESUS  
MACAQUES IN THE CONTEXT OF INSTABILITY

Sam M. Larson

A DISSERTATION

In

Anthropology

Presented to the Faculties of the University of Pennsylvania

In

Partial Fulfillment of the Requirements for the

Degree of Doctor of Philosophy

2019

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## **DEDICATION**

For Jane, and a more empathetic science.

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The data herein represents a long-term effort investigating the genetics of social behaviors in rhesus monkeys, supported by NIMH grants R01-MH089484, R01-MH096875, and the NSF DDIG for Biological Anthropology. The project owes its success to numerous field assistants. Among them, I wish to thank Bonn Aure, Jacqueline Buhl, and Josue Negron for taking the time to train me when I was still bright eyed and bushytailed. Similarly, I wish to thank Andy Daws, Charlie Espinosa, and Fiona Jensen-Hitch for their patience while I was training them when I was...whatever the opposite of bright eyed and bushytailed is. Drunk and defeated? I would not have been able to handle Group R without them.

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## ABSTRACT

### THE AFFILIATIVE SOCIAL RELATIONS OF FREE-RANGING RHESUS MACAQUES IN THE CONTEXT OF INSTABILITY

Sam M. Larson

Dr. Michael Platt

Across primates, socially integrated individuals exhibit improved genetic fitness compared to their peripheral conspecifics. However, the mechanisms through which this disparity operates is unclear. One hypothesis is that social bonds mitigate the stressors imparted by environmental instability. To date, this relationship has gone critically unexamined, owing to the inability to anticipate and account for instability in prospective research design. In this dissertation, I evaluate this hypothesis within a population of free-ranging rhesus macaques (*M. mulatta*). I employ a long-term behavioral data set comprised of 691 unique individuals across 6 groups, followed from 1 to 8 years. I employ the tool-kit of social network analysis to integrate social phenotypes at the individual, dyadic, and group-level. I examine two destabilizing events. First, I examine how affiliation patterns precede a matrilineal overthrow, an outburst of aggression which resulted in group dissolution. As a prelude to this analysis, I investigate the manifestation of rank instability more generally, and, in concert with other dimensions of social life, examine its relationship to psychosocial stress. Second, I examine affiliation in the wake of environmental disaster: here, that of Hurricane Maria, which in 2017 had caused near-complete deforestation. I find that instability leaves an enduring signature in expressions of psychosocial stress. In the context of instability, monkeys show critical transformations in their affiliative patterns — in frequency, variability, and direction — but in ways highly dependent on the type of instability experienced. Such transformations are not experienced uniformly across social units, but instead are concentrated upon those most likely to suffer (or endure) the costs of that



instability. This analysis indicates that rhesus monkeys exhibit considerable social flexibility in response to environmental instability and that social bonds, rather than static, are continually renegotiated. Destabilizing events are rare but can impart instantaneously brutal fitness consequences. It is critical, then, that we accumulate case studies of their effects —messy though they may be — to avoid blind spots in our understanding of the evolution of social bonds.

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# CHAPTER 1

## AFFILIATIVE RELATIONSHIPS IN THE CONTEXT OF DISASTER: AN INTRODUCTION

### INTRODUCTION

Compelling evidence across human and nonhuman primates indicates poor social status as a risk factor for numerous kinds of pathologies and, by extension, poor genetic fitness (Sapolsky, 2004; Silk, 2007a). In humans, social isolation is associated with an increase in mortality that is on par with that from alcohol and tobacco use (Holt-Lunstad et al., 2010; Yang et al., 2016; Courtin and Knapp, 2017; Elovainio et al., 2017). In baboons (*Papio* sp.) females with strong, enduring social bonds live longer (Silk et al., 2010; Archie et al., 2014) and have offspring that more often survive to the age of first reproduction (Silk et al., 2003, 2009). Similarly, in rhesus monkeys (*Macaca mulatta*), strong social bonds correspond to greater reproductive success (Brent et al., 2013a) and lower mortality (Brent et al., 2017a). Male Assamese macaques (*M. assamensis*) that form close social bonds make speedier ascensions of their dominance hierarchies and secure greater reproductive access (Schülke et al., 2010). Similar effects have been demonstrated in multiple taxa outside the Order Primates (Ryder et al., 2008, 2009; Cameron et al., 2009; Frère et al., 2010; Lea et al., 2010; Strauss and Holekamp, 2019), showing a clear adaptiveness of social bonds.

The means through which social bonds contribute to these fitness disparities is no doubt etiologically complex. One perspective sees social investments as a means of mitigating environmental stress (Dunbar, 2010). Among nonhuman primates, being with others is associated with a decelerated heart rate (Aureli et al., 1999; Grandi and Ishida, 2015), the release of endorphins (Keverne et al., 1989; Martel et al., 1995; Graves et al., 2002), reduced levels of stress hormones (Wittig et al., 2016), and reduced levels of conspicuous behavioral signals of stress (Aureli and Yates, 2010). A critical means through which nonhuman primates invest into social bonds is through allogrooming, the removal of debris from the fur of a conspecific. In many cases, it is the gift of grooming more so than its receipt that show these mollifying effects, indicating the act of investment *per se* and separate from the mere presence of support is important (Barrett et al., 1999; Henzi and Barrett, 1999; Shutt et al., 2007). In other words, it is not the quantity, but the quality of bonds that makes this determination (Cheney and Seyfarth, 2009).

In the context of disaster—that is, an event that prompts a group to make facultative adjustments lest it no longer endure—the benefits of social bonds are especially salient. In humans, the presence of social support networks in the wake of disaster can provide resilience to the development of the physical (Ruggiero et al., 2009) and mental (Brewin et al., 2000; Ozer et al., 2003) disorders so frequently observed in tow. However, limited evidence exists for this pattern in free-ranging, non-human primates. The most researched model of disaster among multi-male, multi-female groups of *cercopithecine* primates is the immigrant male takeover, which can cause considerable instability in the prevailing dominance hierarchies and introduce the threat of infanticide for females with recent offspring (Sapolsky, 1992, 2005; Sapolsky et al., 1997; Bergman et al., 2005). In this context, female baboons (*P. hamadrayas*) that focus their



social bonds on a small group of reciprocating females show muted stress responses to male hierarchical instability and faster returns to baseline compared to females that are weakly bonded with diverse partners (Wittig et al., 2008a). This quality of social bonds is also shown to be associated with reduced stress in times of relative stability (Crockford et al., 2008).

Despite the clear adaptiveness of social bonds, however, is unclear whether individuals will make these investments in the context of disaster (Strier, 2017). Among nonhuman primates, the ostensible pattern is much the opposite. Past research has largely considered two ways in which social relations might transform to accommodate changing externalities in nonhuman primate groups (Dunbar, 1991, 1992). Social bonds are an investment. As such, are expected to trade-off with other time and energy intensive activities. If a destabilizing event, say a natural disaster (Behie and Pavelka, 2012; Russon et al., 2015), resulted in the decimation of a critical food source, than it would be anticipated to impact all individuals equally, causing global reductions in social behaviors (Negrín et al., 2016). In humans, the depletion of resources concomitant with disaster can exacerbate social inequalities (Molotch, 1970; Bond, 2013), and place strain on existing social relations (Drescher et al., 2014). Humans are frequently observe to shift focus toward their immediate needs if they feel their current environment is unreliable (Griskevicius et al., 2011; Kidd et al., 2013); when they can operate from a place of security, they are more likely to exhibit prosocial behaviors (Bin and Edwards, 2009; Vardy and Atkinson, 2019). Instead of global reductions in the frequency of interactions, nonhuman primates may change their choice in partners, redoubling their social investments in those bonds that are most likely to impart stress mitigating effects, those with their closest kin. Such an effect is visible in the context of instability caused by increasing group size, where individuals may be unable to service all other individuals and maintain group cohesion (Henzi et al., 1997; Lehmann et al., 2007).

## PRECIS OF THE DISSERTATION

In this dissertation, I examine the transformations of affiliative social networks exhibited by free-ranging rhesus monkeys of Cayo Santiago island in the contexts of destabilizing events. To do this, I employ a long-term behavioral data set comprised of eight years of continuous focal observation for 692 individuals parsed into six social groups. Within these focal follows, I examine all incidences of social behaviors, e.g., allogrooming and aggression. I apply the tool-kit of social network analysis (SNA) to these interactions to characterize and integrate the social phenotype at the individual, dyadic, and group level. I take as case studies two destabilizing events to occur on the island. The first is a matrilineal overthrow that had occurred in early 2012. Following a focused period of instability within the female dominance hierarchy the alpha-family of females was evicted into two daughter groups; nearly half of these evicted females would die within the immediate weeks. In **Chapter 2**, I investigate the phenomenon of dominance instability more generally: I validate a recently developed, network-based measurement of rank instability in our sample by examining its distribution through the population. I parse the effects of rank instability from rank position and social integration on three measurements—two behavioral and one morphological—of psychosocial stress. I further examine if the quality of being unstable in rank is a feature recognized by others, as evidenced by conspecific changes in behavior when approached by an individual of unstable rank, compared to when approached by one of stable rank. In **Chapter 3**, I investigate the affiliative and agonistic social networks in the two years preceding the matrilineal overthrow. I test explicitly, the hypothesis that, with the presumption of rising levels of instability within the group as the overthrow became nearer in time, females transform their social relations to preempt the overthrow. I examine both alterations in the frequency of grooming and aggression interactions as well as changing patterns of the direction of these interactions, within and

between matrilineal females. Finally, in **Chapter 4**, I employ a second case study to examine the role of social bonds in mediating the stress imparted in the wake of environmental disaster. In late 2017, Hurricane Maria had crossed the island of Cayo Santiago, resulting in a near-complete deforestation of the site. In this dramatically transformed landscape, I examine how social interactions transform to mediate the loss of a critical resource. Owing to necessary changes to how data was collected in the post-hurricane period, I focus on proximity interactions between individuals. As with the matrilineal overthrow, I examine changes to both the frequency and choice of proximity partners. Additionally, with the presumption that investments into social bonds comes at a cost, I examine what individuals are most likely to pay those costs; that is, show the greatest increases in investment post-hurricane. Finally, in **Chapter 5** I synthesize across case studies and discuss implications of instability for the general study of primate behavior. Owing to the extreme rarity of these destabilizing events, I am proffered a precious purview into the role social bonds play in the wake of disaster, whether they be within social or environmental spheres.

## **STUDY SPECIES**

The rhesus macaque is a cercopithecine (old-world) primate with wide geographic distributions across continental south and east Asia (Thierry, 2007; Figure 1.1). They live in multi-male, multi-female groups of variable size. Behaviorally, they are among the most despotic macaque species: they are highly aggressive and show the lowest amounts of conciliatory tendencies (Thierry, 2000); grooming partnerships are highly structured by status and genetic relatedness (Sueur et al., 2011b). Aggression exists in highly linearized dominance hierarchies that are largely independent for males and females (Datta, 1988). For males, dominance rank is highly malleable across the life-course and depends on their ability to remain physically competitive.



**Figure 1.1 Rhesus macaque adult female (ID: 3B8) with recently born offspring.** Photograph by Sam Larson

For females, dominance rank is inherited maternally and depends more on the ability of closely related families to compete. Females are also the philopatric sex and will remain in their natal group their entire lives; these qualities combine to make them the enduring core of social groups (Larson et al., 2018). Males will disperse from their natal groups upon reaching sexual maturity and travel between groups multiple times throughout their lives (Trefilov et al., 2000; Brent et al., 2017b). Recently migratory males generally enter new groups as subordinates, with rank ascension corresponding with increase in tenure (Berard, 1999), although more aggressive takeovers from migratory males are also observed (Georgiev et al., 2016). Reproductive access is highly skewed towards the alpha-male, but there are also high levels of covert copulations from subordinate males (Nurnberg et al., 1994; Overduin-De Vries et al., 2012); the relationship

between dominance rank and fitness is attenuated in females, who show considerably less variation in their mortality and fertility rates.

Rhesus macaques are a particularly well suited model for the present research question owing to their impressive behavioral flexibility, and ability to facultatively transform their behaviors in response to changing externalities (Strier, 2017). For example, rhesus monkeys not only endure, but thrive, in human transformed landscapes. This particular quality had earned them the sobriquet of the “weed” macaque (Wolfe and Peters, 1987; Richard et al., 1989), and is a critical point of difference with most other primates, whose continuance is threatened by human encroachment and climate change (Riley, 2018). In Asia, large numbers of rhesus groups are observed living at least partially within the umbra of urban areas (Southwick and Siddiqi, 1994). For this reason, rhesus monkeys at times have been classified as an invasive species, having established troops in the U.S. (Riley and Wade, 2016; Anderson et al., 2019) and mainland Puerto Rico (Engeman et al., 2010). This feature is likely why rhesus endure in captive settings, contributing to its prominence in human biomedicine (Ahuja, 2013). Their success owes to their behavioral flexibility. For example, rhesus are diet generalists, and in urban settings are often observed to take advantage of human refuse (Sengupta and Radhakrishna, 2018). Understanding these facultative adaptations that primates make in response to human transformed landscapes is in the purview of the nascent discipline of ethnoprimateology (Fuentes, 2010, 2012; Riley, 2018).

## **FIELD SITE**

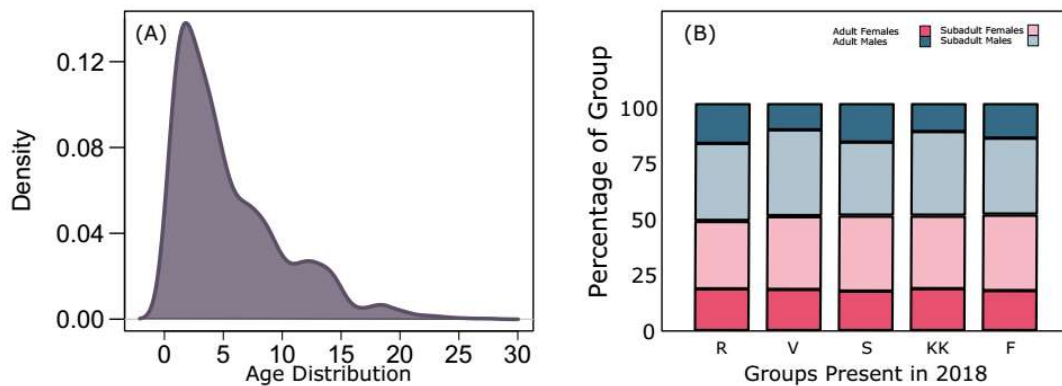
Such species lineaments are on full-display at the field site of Cayo Santiago island, where the work of this dissertation takes place. Located off the coast of mainland Puerto Rico (18°09'N, 65°44'W; Rawlings & Kessler 1986), Cayo Santiago island has accommodated a free-ranging

population of rhesus monkeys since 1938 following their initial transposition from Asia (Montgomery, 2005; Kessler and Rawlins, 2016), placing it among the largest continuously reproducing populations under scientific investigation. As of 2018, this population is considerably young (median age: 3.83; Figure 1.2 Panel A); a feature that signifies a recent acceleration of the population growth rate (Hernández-Pacheco et al., 2016a; b). The population currently aggregates into five social groups, a number that has varied significantly across the species' occupancy (Chepko-Sade & Sade, 1979; Figure 1.2 Panel B).

The animals are artificially provisioned with commercial monkey chow and water *ad libitum*, which monkeys supplant with natural vegetation on the island. Individuals are identified through a unique alphanumeric tattoo placed on their chest and inner thigh, as well as through artificial ear-notches. Beyond intermittent inoculations with the purpose of controlling for diseases like tetanus and tuberculosis (Kessler et al., 2015), the monkeys receive no medical intervention of any kind, and are subject to no predation. Owing to the remarkable access such a setup can afford, the rhesus of Cayo Santiago have functioned as a kind of “living laboratory,” and have figured prominently in research from a variety of disciplines, including genetics (Widdig et al., 2016), kinship (Berman, 2016), cognition (Drayton and Santos, 2016), and human biomedicine (Ahuja, 2013).

## **BEHAVIORAL AND DEMOGRAPHIC DATA COLLECTION**

The behavioral data employed herein has been collected as part of a long-term study of genetic contributions to social behavior. Behavioral data were collected in 10-min focal follows under a 50-behavior ethogram using a Teklogic Psion WorkAbout Pro. In these samples, all affiliative (e.g., grooming), agonistic (e.g., contact and non-contact aggression) behaviors were recorded,



**Figure 1.2 Population of age distribution (A) and operational sex ratio per group (B), as of 2018.**

along with partner ID and duration. Additionally, scan samples, in which all individuals within 2m of the focal subject are evaluated, were conducted at the 0, 5, and 10-min mark in each focal sample. Focal samples were balanced across six-time blocks in order to account for temporal variation in behavior. Since the inception of behavioral data collection in 2010, the project has expanded to include ca. 700 unique individuals from six social units, totaling over 6000 hrs of observation.

## **SOCIAL NETWORK ANALYSIS IN PRIMATOLOGY**

Group-living primate individuals show clear heterogeneity in their affiliative and aggressive tendencies (Seyfarth et al., 2012; Brent et al., 2014b), which nonrandomly configure them into multifaceted global networks (Krause et al., 2009). A useful development in the study of this complex sociality has been the recent adoption of social network analysis (SNA) (McCowan et al., 2008; Wey et al., 2008; Sueur et al., 2011a; Makagon et al., 2012). SNA is an analytic

approach to a graphical representation of population structure, or sociograms, which model the actors (nodes) of a system and the relationships (edges) between them (Croft et al., 2008). The strength of SNA lies in its ability to examine and integrate information at the individual, dyadic, and global levels; from individual phenotype to the emergent properties of a system. For these reasons, SNA has been able to advance knowledge in several domains of primate sociality: parsing important from unimportant individuals in social groups (Ramos-Fernandez et al., 2009; Crofoot et al., 2011; Gilby et al., 2013), captive management and well-being (McCowan et al., 2008; Clark, 2011; SCHEL et al., 2013), identifying sub-community structure (Mac Carron and Dunbar, 2016; Feldblum et al., 2018; Larson et al., 2018), describing the spread of disease (Naug, 2008; Balasubramaniam et al., 2018) or, in humans, cultural practices (Christakis and Fowler, 2007, 2008; Fowler and Christakis, 2008; Balbo and Barban, 2014), and elucidating the often invisible importance of indirect connections (Brent, 2015).

For social behavior, for it to have evolved by natural selection, there must be at least some heritable genetic basis. Studies in animal and human social networks indicate that involvement in both the affiliative (Fowler et al., 2009; Brent et al., 2013a) and aggressive (Fairbanks et al., 2004; Lea et al., 2010; Yeh et al., 2010) domains of group life is predisposed in part by additive genetic variance. If social dispositions are predisposed by genetics, then non-randomly distributed phenotypes in a network should also extend to genotypes. Endorsing this hypothesis, allelic variation of serotonergic genetics is associated with grooming network centrality in rhesus monkeys (Brent et al., 2013a). In human and nonhuman primate networks, relationships are more likely formed between those who are similar in phenotype (McPherson et al., 2001; Massen and Koski, 2014), a pattern that has been shown to extend to the genotype (Fowler et al., 2011; Christakis and Fowler, 2014).



## **CHAPTER 2**

### **THE SIGNATURE OF RANK AND RANK STABILITY IN THE CONSPICUOUS SIGNALS OF PSYCHOSOCIAL STRESS**

#### **INTRODUCTION**

In many primate groups, individuals will, through their agonistic interactions, jockey for position within a global dominance hierarchy. Being of high rank is known to impart numerous benefits, including food (White and Wood, 2007; Foerster et al., 2011) and reproductive access (Majolo et al., 2012), increased affiliative attention from conspecifics (Snyder-Mackler et al., 2016), and improved overall health (Archie et al., 2012; Lea et al., 2018). Concomitantly, being subordinate is frequently associated with being stressed (Sapolsky et al., 1997; Sapolsky, 2005). This relationship is heightened among males (Coe et al., 1979; Sapolsky, 1992) and attenuated or non-existent among females (van Schaik et al., 1991; Weingrill et al., 2004; Nguyen et al., 2008). This difference owes to the greater levels of intra-sexual competition exhibited by males relative to females, and that, for males, the relationship between rank and reproductive access is more certain (Majolo et al., 2012). Finally, the relationship between stress and subordination is particularly visible among species that display greater levels of despotism and place a greater importance on kinship in structuring interactions (Abbot et al., 2003).

Although rank is a critical determinant of stress levels within primate groups, it is not the only dimension of the dominance hierarchy to exert an effect. Just as subordination is stressful, so

too is the mere threat of subordination. Dominance rank, rather than being a static entity, is something that is continuously renegotiated between conspecifics, and reversals of rank do occur. The stability of dominance rank can show considerable variation within and between populations. For example, among *cercopithecine* primates, male dominance rank tends to be more unstable than that of females. For females, the philopatric sex, rank is inherited nepotistically and endures across the life-course (Datta, 1988). For males, who leave their natal groups upon reaching sexual maturation, rank is associated with their ability to aggressively compete, with the result being that they more often experience violent rank reversals. There is also considerable inter-species variation in rank reversals, with some species, like rhesus macaques (*M. mulatta*), showing considerably greater despotism and more violent takeovers (Thierry, 2007; Sueur et al., 2011b). Finally, within a species, the rigidity of dominance rank can be imparted by the personality types of central individuals (Sapolsky and Share, 2004).

Rank instability is challenging to study through prospective research design as it is often unanticipated. Traditionally, past research employed situations in which rank instability is highly visible, for example, the deposition of an alpha-male through immigrant takeover (Sapolsky, 1992; Bergman et al., 2005; Wittig et al., 2008a), or a clear, undisputed rank reversal (Setchell and Dixon, 2001). However, prediction of instability is currently being facilitated by the identification of certain behavioral and demographic predicates. For example, instability is anticipated to increase in frequency with the number of high-ranking natal males, that is, with males just entering the sexual market but who still possess large amounts of kin support (Beisner et al., 2011a; McCowan et al., 2018). This can be of issue for captive population where the normal patterns of dispersal are disrupted. In free-ranging macaques, males with high-ranking mothers are more likely to delay natal dispersal (Koford, 1963; Rawlings and Kessler,

1986; Weiß et al., 2016), engendering this unstable confluence of demographic features. There is some evidence to suggest this is true also for females entering the sexual market (Samuels and Henrickson, 1983a).

A second feature frequently observed to lead to rank instability is low average genetic relatedness. Rhesus macaque groups are highly structured by kinship (Thierry, 2007; Sueur et al., 2011b). Matrilines that grow large and exhibit low average relatedness are characterized by greater rates of wounding and aggression, as well as more parsimonious grooming (Beisner et al., 2011b).

Finally, rank instability might follow when high-ranking individuals are precluded from performing policing behaviors that can stave the outbreak of more extreme forms of aggression. For example, the experimental removal of high-ranking individuals from a population of pig-tailed macaques (*M. nemestrina*) resulted in grooming, play, and proximity networks that were highly clustered, a finding the authors had interpreted as the consequence of policing behavior having a multilevel impact on group structure (Flack et al., 2005, 2006). Indeed, the mere presence of the highest-ranking individuals can dissuade aggression from subordinates (Oates-O'Brien et al., 2010; Wooddell et al., 2017; McCowan et al., 2018). The performance of these behaviors by a select few, which can encourage, dissuade, or transform the behaviors within others, are termed social niche construction (Odling-Smee et al., 1996; Boehm and Flack, 2010).

Animals may try to negotiate their position within a dominance hierarchy without it resulting in any obvious rank reversals; thus much of this form of instability goes largely unexamined by researchers. In the present study, we evaluate rank and suffused rank stability as separate dimensions of the dominance hierarchy. To do this, we make use of recently developed network methodologies that assess the stability of rank without any overt catalyst for that instability

(Fushing et al., 2011a). We employ a large behavioral data set spanning eight years of observation of a semi free-ranging colony of rhesus monkeys residing on Cayo Santiago island. We examine nearly 700 unique individuals from six social groups. We first examine the independent effects of rank, rank stability, and social integration on three conspicuous signals of psychosocial stress: self-directed behaviors (SDBs), vigilance, and alopecia (hair loss). We test the hypothesis that being of unstable rank, and thus uncertain of position within a social unit, is associated with increased levels of stress, and that this effect is independent from the effects by absolute dominance rank and social integration. We also examine if rank and rank stability are properties that are recognized by conspecifics in proximity; that is, if individuals will reify through their behavior these qualities of their partners. We further test the hypothesis that partners with unstable ranks are more unpredictable and engender consternation within a focal animal, increasing that animal's rates of SDBs and vigilance.

## **METHODS**

### ***Study Population***

We analyze a semi free-ranging population of rhesus macaques (*M. mulatta*) living on Cayo Santiago island, located off the southeast coast of mainland Puerto Rico (18°09'N, 65°44'W; Rawlings & Kessler 1986). Rhesus monkeys are a terrestrial, cercopithecine primate living in large multi-male, multi-female groups (Thierry, 2007). Males and females exist in largely independent, differentially constructed, linear dominance hierarchies. For females, dominance rank is inherited maternally and enduring across the life course; for males, it is heavily tied to their ability to compete with other males and is extremely variable across the life course. This population has been continuously reproducing since 1938, without medical intervention or contraceptive use, and with routine demographic monitoring. Animals are provisioned daily with commercial feed and water *ad libitum*. There are no natural predators on the island.

### ***Measuring Psychosocial Stress***

Though psychosocial stress, as an internal mental state, is not observable *per se*, it can be reified through physiological, morphological, and behavioral signals. We examine the following indices of psychosocial stress

**Self-Directed Behaviors:** Self-directed behaviors (*e.g.*, self-scratching and -grooming; henceforth SDBs) have traditionally been viewed as a marker of social tension (Maestriperi et al., 1992; Troisi, 2002), with higher rates being observed in the context of social subordination (Kaburu et al., 2012), inter-group encounters (Nunn and Deaner, 2004), and aggression, both as offender and recipient (Schaffner and Aureli, 2002). Group-rates show interspecific variation among cercopithecine primates, with higher rates among species with more strict dominance styles (Lutz, 2018). The performance of these behaviors can be experimentally induced in the context of cognitive testing, and are shown to increase when individuals perform poorly in the absence of reward (Leavens et al., 2001; Whitehouse et al., 2013; Leeds and Lukas, 2018). They positively correlate with hormonal metabolites of stress like fecal glucocorticoids (Ferreira et al., 2018; but see Higham, Maclarnon, Heistermann, Ross, & Semple, 2009). Conversely, the rates of SDBs are observed to decrease in the context of mollifying elements, for example, with the receipt of grooming (Schino et al., 1988) or with post-conflict reconciliatory behaviors (Castles and Whiten, 1998; Judge and Bachmann, 2013; Pallante et al., 2018). Finally, anxiety manipulating, pharmacological interventions have been shown to diminish (when given anxiolytics) or augment (when given anxiogenics) the rate of SDBs in captive rhesus monkeys (Schino et al., 1996). SDBs are in general viewed as a passive consequence of increased autonomic arousal imparted by stress (Troisi, 2002).

**Vigilance:** Group-living primate individuals are expected, at times, to orient themselves to gather information from their physical and social environment. The means through which they do this are termed vigilance behaviors (Treves, 2000; Allan and Hill, 2017). Vigilance is an investment (Warm et al., 2008), and as such is anticipated to be enacted with reservation, based on need, and trade-off with other costly behaviors like allogrooming (Blanchard et al., 2017) and foraging (Favreau et al., 2018). The presence of strong social bonds reduces the need for vigilance investment (Gaynor and Cords, 2012). Across taxa, vigilance is diminished when responsibility for it can be diffused across greater number of individuals (Bertram, 1980; Beauchamp, 2008; Gosselin-ildari and Koenig, 2012). Within a group, peripheral animals show the highest rates of vigilance, a so-called “edge effect” (Jennings and Evans, 1980; Fernández-Juricic et al., 2011). Finally, individuals show reductions in vigilance when in the physical presence of conspecifics, suggesting that affiliatively being near another, especially if these individuals are familiar (Kutsukake, 2006), imparts mental security (Treves, 1998; Stojan-Dolar and Heymann, 2010; Busia et al., 2016). Although traditionally operationalized under its presumed function of threat-detection, vigilance, like SDBs, are quite conceivable as a conspicuous signal of anxious mental states. While SDBs are a passive manifestation of stress, vigilance is a conscious activity undertaken by the individual.

**Alopecia:** Alopecia, or hair loss, is a common condition observed in captive primates. Previously, alopecia had been treated as a signal of poor health imparted by captive living, as it has been associated with poor quality in housing (Beisner and Isbell, 2008; Jolly, 2009; Kroeker et al., 2017) and diet (Swenerton and Hurley, 1980). However, free-ranging populations also show alopecia, where it exhibits seasonality (Isbell, 1995) and is observed as a part of normal senescence. More recent considerations have focused on alopecia as a signal for psychosocial stress, having been associated with greater

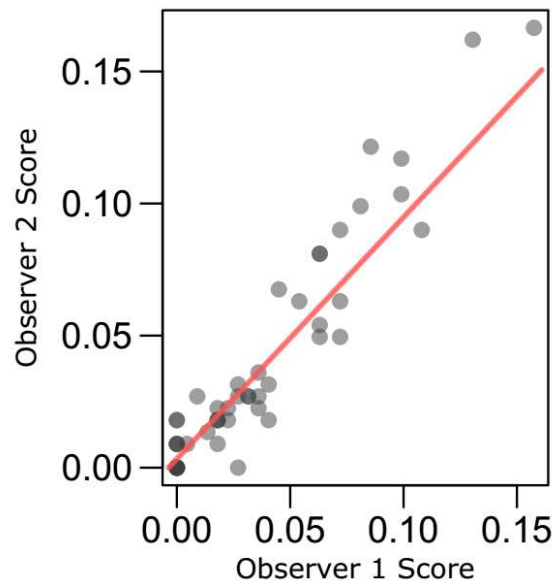
concentrations of hair cortisol (Lutz et al., 2016) and activity of the hypothalamic-pituitary-adrenal axis (Novak et al., 2014). Like SDBs, cercopithecine primates show inter-species variation, with despotic species often showing increased rates of the disorder (Kroeker et al., 2014).

### ***Behavioral and Morphological Data Collection***

Behavioral data were collected in 10-min focal follows under an established, 50-behavior ethogram using Teklogic Psion WorkAbout Pro handheld computers. All affiliative (e.g., grooming), agonistic (e.g., contact aggression), and dominance (e.g., displacement) interactions were recorded along with partner ID and direction. Additionally, scan samples were conducted at the 0-, 5-, and 10-min mark, when the focal animal's state behavior (Feeding, Resting, Grooming, etc.), the ID of all others within 2m of the focal, and their state behaviors were recorded. Both vigilance and SDBs were treated as instantaneous point-behaviors. SDBs were defined as self-scratching or self-grooming (running the fingers through fur for a minimum of 5 seconds). Vigilance was defined as a single turn of the head greater than 45°. Data collection was limited to adults above 6 yrs of age. To control for temporal variation in behavior, focal samples were balanced across six-time blocks. Behavioral data have been collected in this manner continuously across six social groups anywhere from 1 to 8 yrs.

To characterize alopecia among the population, we adapted a procedure developed by Bellanca and colleagues (2014). Here, the subject's body is divided into six discrete zones, each assigned a percentage of the total body: Head and Neck (9), Left Arm (9), Right Arm (9), Back (9), Left Leg (9), Right Leg (9). For each zone, an observer recorded the proportion of that zone affected by alopecia; the summation of each of these scores for each zone, multiplied by their respective proportion of the total body, yields an individualized score for alopecia. Differently from

Bellanca and colleagues (2014), we did not score the chest and inner thigh, as placed at these sites are unique alphanumeric tattoos which are used for identification purposes. All subjects were scored *ad libitum*. Observers were allotted two minutes to score each individual and were instructed only to process individuals under direct lighting, in both a sitting position and in motion. All scores for analysis were conducted by a single scorer in August 2016, during the population's birthing season. A total of 653 unique individuals were scored with this method. Prior to data collection, we estimated interobserver errors with two scorers on 50 animals, finding a high fidelity between observer's recordings (Pearson's  $r = .951$ ; Figure 2.1).



**Figure 2.1 Alopecia scoring interobserver fidelity.** Two observers simultaneously applied Bellanca and colleagues (2014) method for alopecia scoring simultaneously to a set of 50 free-ranging monkeys. Observers show an extreme fidelity between estimates (Pearson's  $r = .951$ )



### ***Data Processing and Statistical Analysis***

We use the tool-kit of social network analysis to characterize individual social position within predominating group structure (Krause et al., 2009; Brent et al., 2011; Brent, 2015). To calculate *dominance rank*, we used a computational approach (Fushing et al., 2011a) in the R package *perc*, which employs knowledge of direct and indirect dominance interactions to arrive at a ranking that maximizes the consistency of the flow of information through the hierarchy. This procedure was performed with matrices that contained all pairwise instances and directions of contact and non-contact aggression, displacement (whereby a dominant individual supplants and takes some resource from a subordinate), and threats (here defined as open-mouthed barking). Using this procedure, we created linear dominance hierarchies independently for males and females in each group in each year. *Dominance rank* was calculated as the percentage of same-sex individuals dominated. Additionally, this procedure also generated a measure of *rank stability*, which incorporates the degree of reciprocity that exists within an individual's direct and indirect connections; individuals that see their agonistic interactions more likely to be returned are said to be more rank "unstable." *Rank stability* was measured on a scale of 0.5 – 1, with higher values being associated with greater rank stability.

We analyzed three additional network types in our analysis. First, we examined proximity networks, generated from our instantaneous scan samples interspersed through focal follows. We calculated the weighted proximity network *eigenvector centrality* as a general measure of how often these individuals were seen near others. We also examined weighted grooming networks of pairwise grooming interactions (s/hr). For everyone, we calculated a *grooming rate* of the seconds per hour they were observed in a grooming state (as donor or recipient). Proximity is a critical prerequisite of grooming interactions (Farine, 2015), and were thus expected to be highly correlated. To better discriminate grooming from proximity networks, we

excluded all instantaneous scan samples in which the focal animal was in a state of grooming; that way, these networks were not necessarily or unavoidably correlated. Finally, we examined aggression networks based on the rates of contact (biting, grabbing) and non-contact (chasing) aggressions. We calculated for each individual *aggression given (out-strength)* and *aggression received (in-strength)*.

First, we created what we term “resting rates” of SDBs and vigilance. To do this, we parsed all focal follows into discrete periods in which the focal animal’s state behavior was recorded as resting, their location was recorded as outside the feeding corral, and there were no other monkeys within 2m of their person. Our goal here was to limit, control, and ultimately examine these immediate, extraneous factors that very likely shape a monkey’s display of these behaviors. We excluded all periods that endured less than 40s; furthermore, we excluded the first 10s of each period to account for transitioning effects between state behaviors and locations. Finally, we excluded all periods from focal follows that contain, at any time, contact or non-contact aggression, given or received. Across these periods, we calculated the sum of their durations and count the frequency of displays of SDBs and vigilance that occur within them, and use these to generate their hourly resting rates. We do this for every individual for every year of their observation.

As we added the recording of vigilance behaviors two yrs into our data collection protocol, it has a slightly smaller sample size. Compartmentalizing our data in this way yields for self-directed behaviors 59217 unique periods, totaling 3785 hrs across 672 individuals, and for vigilance 54077 periods, totaling 3428 hrs, across 622 individuals. We used generalized linear mixed models (GLMMs; Bolker et al., 2009) for significance testing. We initially used GLMMs to assess pairwise fidelity between our measures of psychosocial stress, with *group*, *study year*, and *ID*

included as random effects. We then constructed three GLMMs for each of our measures of psychosocial stress, with our six social dimensions, along with age and sex, as fixed effects; again, we include *group*, *study year*, and *ID* as random effects.

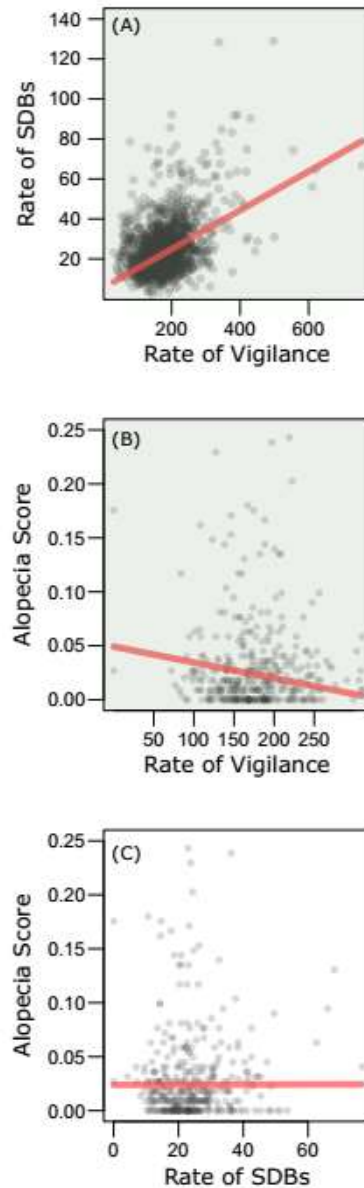
Next, we examined whether dominance rank and rank stability were qualities that focal animals could recognize within proximity partners and reify within their own behaviors. To do this, we focused on the rates of SDBs and vigilance to the exclusion of alopecia, as the former are better equipped to index the current context of an individual. We examined periods in which focals were observed in the presence of one other conspecific. We further classified that conspecific into one of four categories based on two Boolean variables (*low ranking and stable*, *low ranking and unstable*, *high ranking and stable*, *high ranking and unstable*; the order of these classes putatively reflects greater danger within the proximity partner). When the focal animal's proximity partner is same-sex, we use the difference in dominance rank to determine if the proximity partner should be classed *high (low) ranking*. When the focal and proximity partner were opposite-sex, we use the partner's absolute ranking to class them as *high (low) ranking*, with partners that outrank 80% of same-sexed individuals in their group classed as *high ranking*. Proximity partners with rank stability scores greater than 0.8 were classified as *stable*, regardless of their and the focal animals' sex. Focal SDB and vigilance rates were investigated in the context of four GLMM models each, one model for each potential pairing of the sexes, with partner rank and partner stability as Boolean variables. *ID* and *Group* (in the case of males, the group in which they were predominantly found across study years) were included as random effects.

## RESULTS

We found considerable fidelity between our behavioral measures of psychosocial stress: individuals for which we observed high rates of SDBs were also hypervigilant (Est. (SE): .01 (.006); Chisq = 296.01; p-value <.001; Figure 2.2: Panel A). We also found a significant negative relationship between vigilance rates and alopecia scores, such that those with the most hair-loss invested less into social monitoring (Est. (SE): -1.467e-04 (5.66e-05); Chisq: 6.63; p-value = .009; Figure 2.2: Panel B). We found no significant association between the rate of SDBs and alopecia scores (Est. (SE): 6.08e-06 (2.44e-04); Chisq: .0006; p-value = 0.98; Figure 2.2: Panel C).

We found that including an interaction effects between dominance rank and sex, and rank stability and sex improved model fit for SDBs ( $\Delta AIC = -1.9$ ; chisq = 5.88; p-value = .05), vigilance ( $\Delta AIC = -4$ ; chisq = 17.585; p-value <.001), and alopecia scores ( $\Delta AIC = -34.7$ ; chisq = 40.73; p-value <.001). The inclusion of the interaction between dominance and rank certainty did not improve upon our models for SDBs ( $\Delta AIC = 3$ ; chisq = .493; p-value = .78) and vigilance ( $\Delta AIC = 2$ ; chisq = .93; p-value = .63); although it did significantly improve upon our model for alopecia ( $\Delta AIC = -5.2$ ; chisq = 9.24; p-value = .009). All subsequent reports employ the best performing models for each of our stress measures.

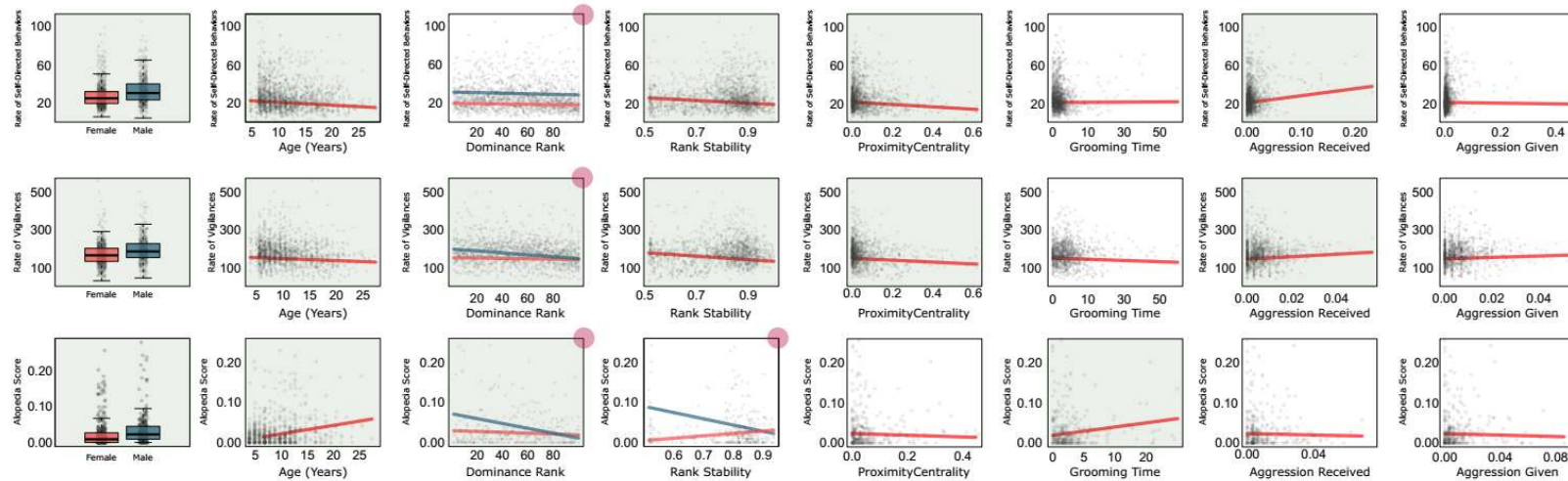
Our two behavioral measures of psychosocial stress index similar dimensions of social life and demography in that young males that are rank subordinate, rank unstable, socially isolated, and receive higher levels of aggression showed the highest levels of SDBs and Vigilance (Table 2.1; Figure 2.3: Top and Middle Rows; Figure 2.4). For both micro-movements, we also observe significant interaction effects between dominance rank and sex, in that this negative relationship was more pronounced in males.



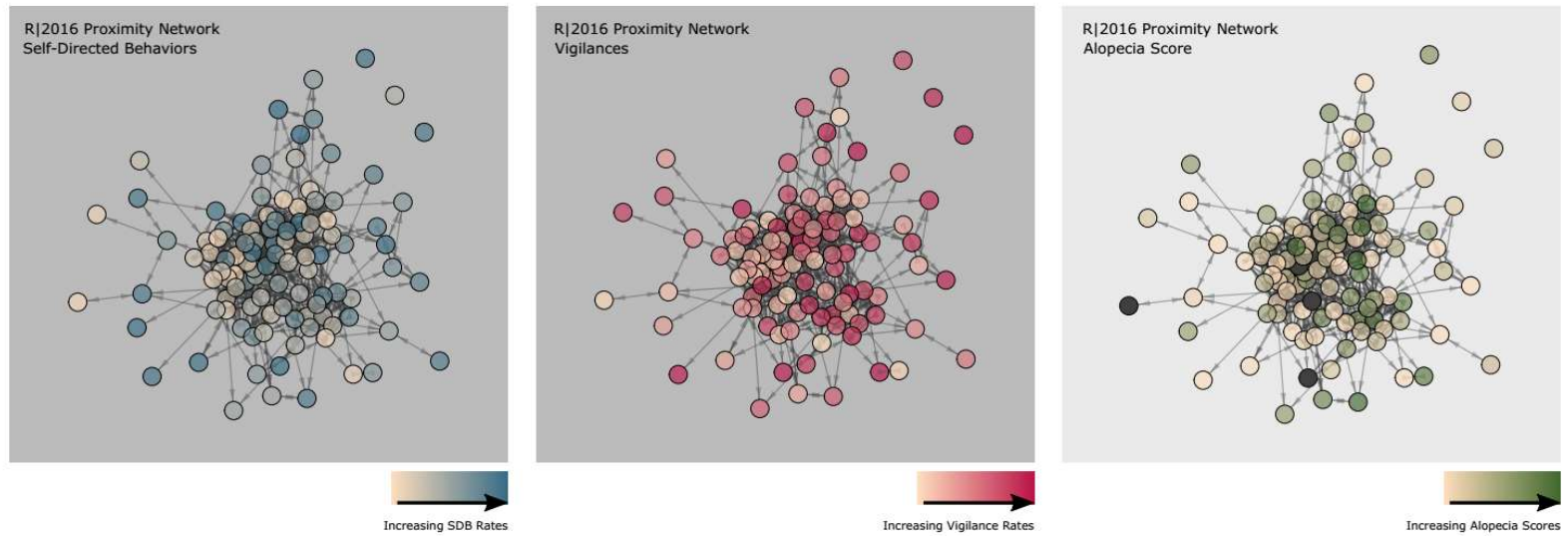
**Figure 2.2 Fidelities of three measures of psychosocial stress.** We examined the pairwise linear relationships between our three measures of psychosocial stress in the context of generalized linear mixed models, with *group*, *study-year*, and *ID* as additional random effects. The positive relationship between the rates of SDBs and vigilance (A) and the negative relationship between alopecia score and vigilance (B) were statistically significant, which we highlighted with a green background.

Fixed Effects	Self-Directed Behaviors			Vigilance			Alopecia Scores		
	Est (SE)	Chisq	p-value	Est (SE)	Chisq	p-value	Est (SE)	Chisq	p-value
Sex	4.07 (4.58)	68.5	<b>&lt;.001</b>	14.96 (18.82)	34.8	<b>&lt;.001</b>	0.418 (0.079)	17.04	<b>&lt;.001</b>
Age	-0.30 (0.08)	12.9	<b>&lt;.001</b>	-1.05 (0.34)	9.4	<b>0.002</b>	0.002 (0.001)	8.36	<b>0.004</b>
Rank	0.004 (0.02)	1.2	0.28	-0.07 (0.07)	14.4	<b>&lt;.001</b>	0.001 (0.001)	10.16	<b>0.001</b>
Rank Stability	-14.03 (4.61)	12.9	<b>&lt;.001</b>	-91.55 (19.48)	20.3	<b>&lt;.001</b>	0.133 (0.061)	0.28	0.6
Proximity Centrality	-12.65 (4.43)	8.2	<b>0.004</b>	-49.82 (18.46)	7.3	<b>0.007</b>	-0.003 (0.048)	0.003	0.95
Grooming	0.01 (0.09)	0	0.91	-0.82 (0.47)	3	0.08	0.001 (0.001)	4.26	<b>0.04</b>
Aggression Received	74.30 (29.01)	6.6	<b>0.01</b>	644.89 (219.55)	8.6	0.003	-0.081 (0.241)	0.11	0.74
Aggression Given	-3.98 (17.71)	0.1	0.82	63.71 (219.35)	2.7	<u>0.1</u>	-0.131 (0.253)	0.27	0.6
Sex*Rank	-0.05 (0.03)	4.7	<b>0.03</b>	-0.43 (0.11)	16.4	<b>&lt;.001</b>	-0.005 (0.001)	6.47	<b>0.01</b>
Sex*Rank Stability	7.31 (5.62)	1.7	0.19	36.92 (23.38)	2.5	0.11	-0.447 (0.097)	15.73	<b>&lt;.001</b>
Rank*RS							-0.001 (0.001)	0.33	0.57
Rank*RS*Sex							0.005 (0.002)	9.09	<b>0.002</b>

**Table 2.1: The influence of social capital on resting rates of behaviors and alopecia scores.** I report the base-models of covariates on the resting rates of self-directed behaviors (SDBs), vigilances, and for alopecia scores. The base model for alopecia contains an additional two-way interaction effect between rank and rank stability, as well as an additional three-way interaction between rank, rank stability, and sex. P-values in bold indicate statistically significant at the .05 level; underlined p-values indicate strongly trending relationships at the .1 level. Grey boxes indicate that these fixed effects were not included in the base models for the respective measure of psychosocial stress.



**Figure 2.3 Impact of social variables on the rates of self-directed behaviors, vigilances, and alopecia score.** Partial regression of the influence of social variables on our three measures of stress, the rate of self-directed behaviors (top row), the rate of vigilance (middle row), and 2016 alopecia scores (bottom row). Green backgrounds indicate relationships that reach statistical significance; purple circles indicate significant interaction effects between the variable of interest and sex

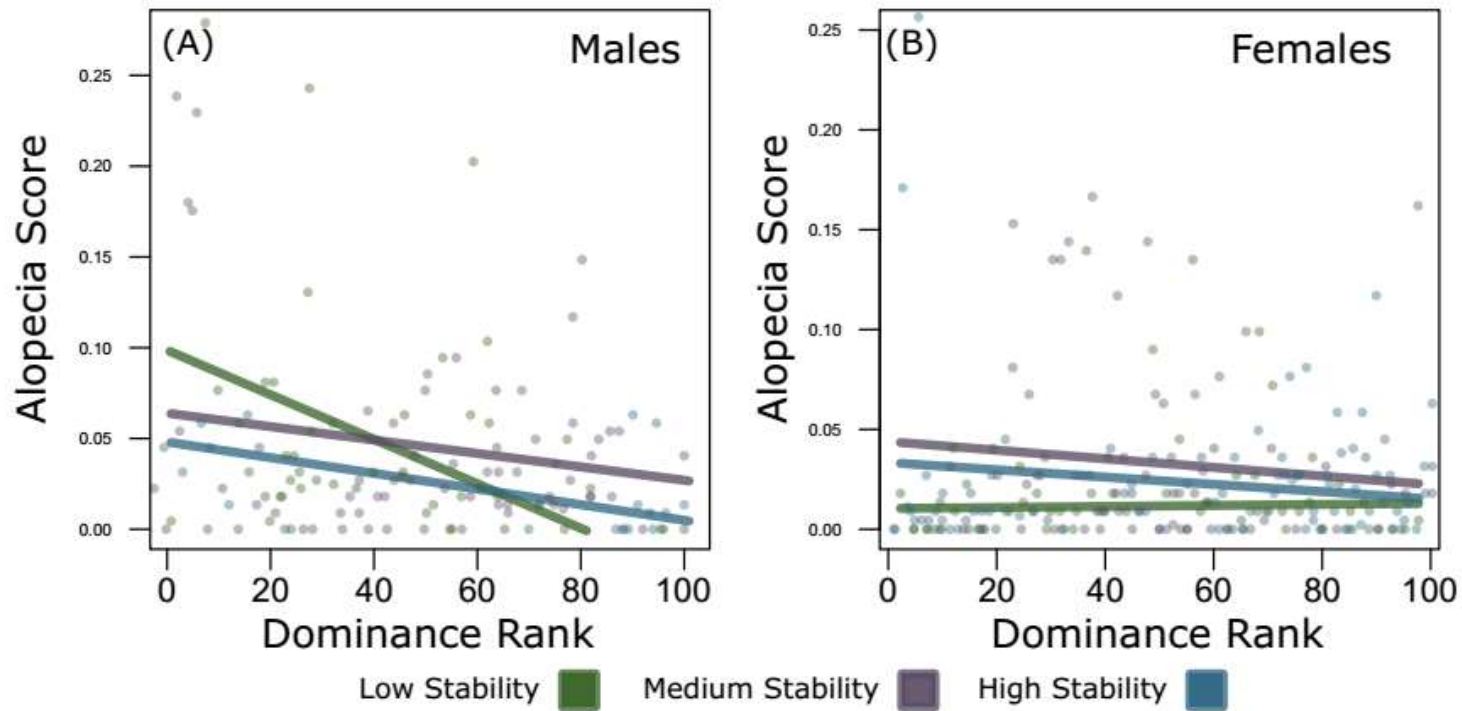


**Figure 2.4 The distributions of phenotypes across the Group R 2016 proximity network.** We plot proximity networks for R|2016, chosen for illustrative purposes. Increasing color intensity indicates increasing rates of self-directed behaviors (blue), vigilance (maroon), and alopecia score (green). Greyed nodes of the alopecia network indicate an absence of data for the individual. Networks with darker panels indicate statistical significance. Network layouts use the Fruchterman-Reingold algorithm.



Like our behavioral measures, alopecia scores showed significant increase in subordinate males (Table 2.1; Figure 2.3: Bottom Row), although this was the extent of their likeness. Alopecia increased with age, likely owing to normal bodily senescence. Alopecia shows a critical interaction effect with sex and rank stability, in that a negative relationship between rank stability and alopecia is observed among males, whereas, among females, this pattern was reversed. Alopecia also showed a significant positive correlation with the amount of time an individual spent in a state of grooming. Finally, we observed a significant three-way interaction effect between rank, rank stability, and sex on alopecia scores. Among males, the negative consequences of being of low rank on alopecia score was especially visible among those with low rank stabilities (Figure 2.5: Panel A). Among females, the negative relationship between rank and alopecia was only observed among those with medium to high degree of rank stability; alternatively, females of low rank stability showed a slightly positive relationship (Figure 2.5: Panel B).

As a *post hoc* analysis, we also evaluated the existence of a *life-at-the-top* effect, whereby the alpha-male, as a special category of individual, showed higher levels of stress (Gesquiere et al., 2011). To do this, we added a dummy variable to our best performing models that described alpha-male status, identifying 14 unique alpha-males across all study groups and periods. We found no relation between alpha-male status on SDB rate (Est. (SE): -1.94 (3.48); Chisq = .31; p-value = .58), vigilance rate (Est (SE): -.78 (14.9); Chisq = .003; p-value = .96), or alopecia score (Est (SE): .02 (.03)' Chisq = .23; p-value = .63).



**Figure 2.5 Three-way interaction between dominance rank, rank stability, and sex.** We observe a significant three-way interaction between dominance rank, rank stability, and sex, on alopecia score. We plot the partial regressions of the relationship between dominance rank and alopecia for males (left-panel) and females (right-panel). We further parsed the continuous variable of rank stability into three quantiles (“Low”, “Medium”, and “High”)

Finally, we found evidence that individuals respond to the rank stability of conspecifics in their proximity (Table 2.2; Figure 2.6). Females showed reduced rates of vigilance when their partner is unstable relative to when they were stable, regardless if that partner was male or female. Females also respond with greater levels of vigilance when their male partner is high ranking compared to low ranking. No such patterns are visible in female SDB rates. Males similarly showed small reductions in both their SDB and vigilance rates when their partners were male and of unstable rank compared to males of stable rank. Males showed no differences considering these variables when they were proximate to a female.

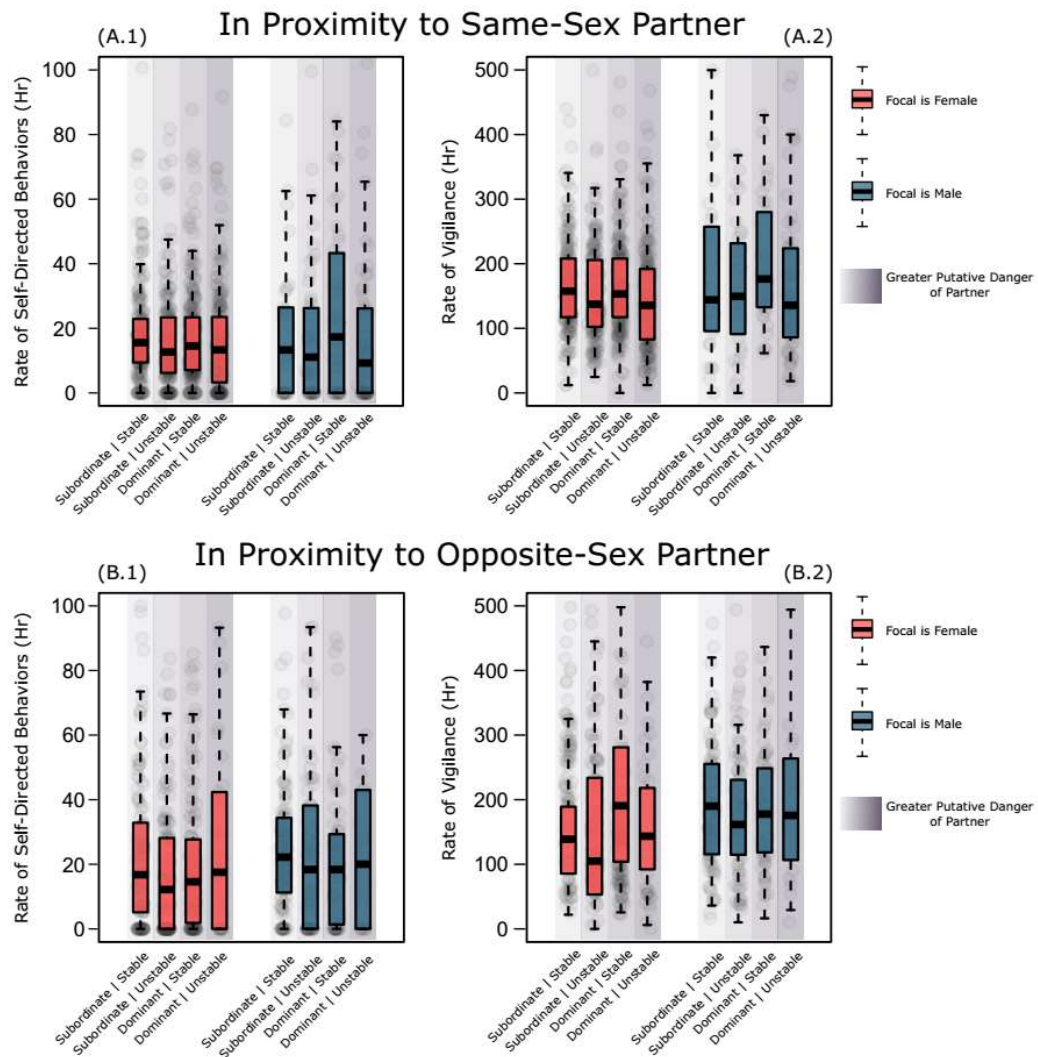
## **DISCUSSION**

In the present study, we examined the role of two dimensions of the dominance hierarchy, absolute rank and rank stability, in the display of conspicuous signals of psychosocial stress. We examined their effects in concert with additional measures of social integration and demography to parse independent effects from each upon these signals. We found an extreme fidelity between SDB and vigilance rates in reifying similar biological dimensions: they are the highest in young males who are subordinate, unstable of rank, are socially isolated, and receive the highest rates of aggression. What is more, the relationship between absolute dominance rank and these micro-movements are intensified in males relative to females, a likely result of greater levels of intra-sexual competition experienced by the former.

That the rates of micro-movements increase with increasing levels of subordination is a familiar finding in primatology (Pannozzo et al., 2007; Gaynor and Cords, 2012). We extend this knowledge by finding evidence that being of unstable rank is independently associated with hypervigilance and agitation. This finding conforms largely to our expectation. Individuals that rank were unstable are more uncertain of their station within a group, and thus face greater

Focal   Partner Sex	Partner Quality	Self-Directed Behaviors			Vigilance Behaviors		
		Est. (se)	Chisq	p-value	Est. (se)	Chisq	p-value
F F	is High Ranking	1.30 (1.78)	1.09	0.3	1.48 (7.34)	0.95	0.33
	Is Rank Unstable	-0.08 (1.92)	0.001	0.996	-16.70 (7.62)	5.41	<b>0.02</b>
	R*Rs	-.15 (2.64)	0	0.96	7.75 (10.64)	0.53	0.47
F M	is High Ranking	-.61 (3.61)	1.31	0.25	44.82 (13.50)	10.07	<b>0.002</b>
	Is Rank Unstable	7.33 (5.48)	0.54	0.46	-5.37 (21.44)	5.7	<b>0.02</b>
	R*Rs	-13.69 (6.57)	4.35	<b>0.04</b>	-29.83 (25.17)	1.4	0.24
M M	is High Ranking	-6.64 (6.46)	1.16	0.28	-4.32 (28.34)	0.01	0.93
	Is Rank Unstable	-9.85 (5.84)	3.62	<u>0.057</u>	-41.35 (25.36)	3.71	<u>0.054</u>
	R*Rs	3.55 (8.66)	0.17	0.68	10.49 (37.48)	0.08	0.78
M F	is High Ranking	3.23 (4.67)	0.16	0.69	-16.60 (16.89)	0.98	0.32
	Is Rank Unstable	9.36 (7.69)	1.53	0.22	-14.17 (26.52)	0.32	0.57
	R*Rs	-6.12 (8.89)	0.47	0.49	8.46 (30.61)	0.08	0.78

**Table 2.2 The influence of partner rank and partner rank stability on focal performance of SDBs and vigilance, parsed by sex.** We report the results of 4 models (one for each combination of focal and partner sex) with proximity partner rank and rank stability included as fixed, Boolean variables, as well as their interaction. Values in bold indicate statistically significant relationships; underlined values indicate strongly trending associations



**Figure 2.6 Boxplots of focal SDB (A) and vigilance rates (B) when with same- (1) and opposite-sex (2) proximity partners.** Boxplots summarize the individualized rates of SDBs (A) and vigilances (B) when female (red boxplots) and male (blue boxplots) focals are observed with same- (1) and opposite-sex (2) partners. Backgrounds of increase color (purple) intensity indicates proximity partners of increasing (putative) danger and uncertainty

ambiguity in their daily life. Individuals of this quality are expected to be hypervigilant from incoming threats, as well as opportunities for advancement, and show commensurate degrees of anxiety in the process.

Alopecia, like our micro-movement measures, shows a similar negative correlation with dominance rank, especially among males; this is however, the extent of their similarities. Different from micro-movements, alopecia increases with age, likely owing to its constituency in ordinary senescence. Alopecia also shows diverging influence from rank stability among the sexes, with increasing stability being associated with healthier coats in males, but unhealthier coats in females. This difference might reflect the limits of interpretation in our social measurements. We measured rank stability as a function of the degree of reciprocity in aggressions that exist after sorting the hierarchy.

While seeing a greater proportion of aggressions returned is indicative of uncertainty of rank, it might also be indicative of personality differences between individuals, particularly in their likelihood of delivering contextually inappropriate aggression. Among females, individuals of certain personality types might be more likely to threaten up the hierarchy, say, if the alpha-female approached their offspring, without that action constituting any challenge to rank. Under this perspective, rank stability measures among females might reflect their own inhibition and activity (and thus positively correlate with their micro-movements), but not their certainty of their group station (and so does not correlate with alopecia). At minimum, this pattern endorses the further development of more nuanced versions of these measurements.

Past primate research has found compelling evidence that instability is more strongly felt by high ranking individuals, who have much more to lose through a descension in rank (Sapolsky, 1992; Gesquiere et al., 2011). In the present analysis, we struggle to find evidence that further endorses this pattern. First, we see no evidence for a life-at-the-top effect among 14 alpha males in their SDB and vigilance rate or their alopecia scores. As this is the first study, to our knowledge, to assess this effect using this suite of measurements, it may be entirely possible that such an effect is simply invisible among them.

We also find in alopecia scores a three-way interaction effect between dominance rank, rank stability and sex, such that males who are both rank unstable and low in the hierarchy show the most intense hair-loss. This is a slightly unanticipated result. In previous research, an interaction effect was shown between these three variables on the levels of inflammatory proteins in captive rhesus, so that high ranking males who were also unstable showed the highest levels of stress (Vandeleest et al., 2016b). The differences between the present study of alopecia and the previous one of inflammatory markers might reflect the time scales over which these two indices of stress manifest, with alopecia being slower to develop. Under this conception, inflammatory proteins might be a more instantaneous response to the prospect of falling in rank, while increased alopecia may be the result of prolonged exposure to uncertainty at lower ranks. A time-series of analysis of rank stabilities with our rhesus population is thus warranted.

Alopecia exhibits an additional point of difference from micro-movement rates. While the latter show reductions with increasing amounts of grooming, the opposite is visible for the former. Rather than an index of social marginalization, alopecia therefore might function as a signal to others for increased attention. Primates are frequently observed to attend to others who had recently received aggression (Romero et al., 2010; Clay and de Waal, 2013), and alopecia might

be a similar impetus for empathy. Elsewhere, it has been shown that Barbary macaques (*M. Sylvanus*) will pay extra attention to the self-scratching of others (Whitehouse et al., 2016), especially if they are weakly bonded. Here, behavioral variation indicates that some information is imparted by SDBs performed by others, although the influence of social distance suggests it might signal avoidance rather than attendance. This is also reflected in that self-scratching exhibits contagious properties (Nakayama, 2004; Palagi et al., 2009; Feneran et al., 2013), where the presence of nervous individuals can presumably make conspecifics nervous themselves. Focused experiments of alopecia as an elicitor of empathy would be profitable.

We find that both rates of SDBs and vigilance decline with age. Within the same population, individuals are seen to retreat from social life in older age classes (Brent et al., 2017b), potentially the result of their own reduced energy expenditure. This shift might also explain the reductions in micro-movement behaviors that we observe here. As our sample only includes individuals who are six years and older, the rates of behaviors among younger age classes goes unseen, missing critical ontogenetic patterns (Alberts, 1994; Allan and Hill, 2017). Across several primate species, juveniles increase their rate of vigilance approaching adulthood (Westoll et al., 2003; Gosselin-ildari and Koenig, 2012; Busia et al., 2016) and decrease it with aging post-maturation (Watson et al., 2015).

We wish to highlight a significant point of difference between this and a previous study of Cayo Santiago rhesus monkey vigilance, conducted by Watson and colleagues (2015). In the latter study, the authors found a positive correlation between dominance and vigilance rates.

Vigilance was studied in the context of drinking water, which, as a more exclusionary resource, might be a more salient arena where dominance relations are tested and secured. Our own observed pattern of dominance and vigilance behaviors is localized to those periods in which the



focal animal is resting, a much less stressful context. This difference speaks to the importance of contextualizing these behaviors as best as possible, as it can lead to diverging conclusions regarding the relationship between these behaviors and social structure.

Another key finding of this study is that rhesus macaques seemingly recognize the stability of rank within their social partners. Previous primate research had indicated that proximity to dominants raises a focal animal's SDB and vigilance rates (Pavani et al., 1991; McNelis and Boatright-Horowitz, 1998; Gaynor and Cords, 2012; Zhang et al., 2014). We find some additional support for this relationship: here, females near high-ranking males exhibited hypervigilance. However, we find a more consistent pattern with partner rank stability, whereby females, regardless of partner sex, and males near other males, show decreased rates of micro-movements when their partner is of more unstable rank. Like absolute rank, this is likely a function of increased uncertainty of the interaction: whether they should be treated as a potential threat, or if they are the target of ire themselves. At first glance, reductions in micro-movements would suggest that being with unstable individuals is *less stressful* than being with those who are stable. However, we believe the more likely explanation is that proximity to unstable individuals is producing freezing behavior in focal animals. In addition to "fight" or "flight," extremely stressful situations can also produce a cessation of movements more generally. In our study, we have employed, relative to other research, a conservative criterion for proximity (2m), and such closeness might prove more stressful than we anticipated. In the context of a potentially dangerous individual, a focal animal's attention might focus upon that individual only and produce the hypovigilance that we have been interpreting elsewhere as indicating security. Thus, we suggest caution in interpreting this finding. Future studies should

be wary of their operationalization of proximity, with best practices being examining how variance in conspecific distance influences a focal animal's behavior.

In this study, we have found evidence for the independent influence of absolute dominance rank and rank stability—subordination from the threat of subordination—on the visible signals of stress in free-ranging rhesus monkeys. In primate hierarchies, in rhesus or otherwise, individuals continuously renegotiate their status, but not all attempts of ascendancy result in rank reversals. In this study, we have employed a network-based procedure that can capture these rank negotiations as they occur in day-to-day life, without any obvious catalysts for instability, making it a potentially powerful tool in understanding instability. This procedure does have certain limits: it cannot, for example, parse focal instability caused by challenges emanating from or towards that focal. Nevertheless, in the future, incorporating this measure of suffused dominance instability, we believe, will prove profitable for understanding primate social systems.

## **CHAPTER 3**

### **NETWORK DYNAMICS PRECEDE AND FOLLOW A MATRILINEAL OVERTHROW IN RHESUS MACAQUES**

#### **INTRODUCTION**

Animals that live in groups are faced with the challenge of balancing the benefits of group living with the costs of conflicting interests between group mates (Krause and Ruxton, 2002; Silk, 2007b). Balancing these costs and benefits may be especially difficult for individuals that live in groups composed of both kin and non-kin (Seyfarth and Cheney, 2012). Much theoretical and empirical research has focused on how individuals may use aggression, social status, cooperation, and social bonds to cope with intra-group conflict; yet, a great deal about the origins and maintenance of group-living remains unclear (Krause and Ruxton, 2002; Nowak et al., 2010; Shultz et al., 2011; Brent et al., 2014a). Network dynamics within groups can reveal the processes that underpin the structuring of animal societies and can uncover information about the adaptive functions of social behaviors and relationships (Flack et al., 2006; Bode et al., 2011; Crofoot et al., 2011; Pinter-Wollman et al., 2014). Describing dynamic shifts in social networks and determining when and why these shifts occur is therefore an important route to understanding the maintenance of social groups and the evolution of sociality generally.

A growing number of studies have documented network dynamics within groups that have followed changes to the physical environment. For example, association networks become more

tightly connected when resources are scarce in killer whales (*Orcinus orca*: Foster et al., 2012). This finding is in accordance with the hypothesis that prosocial relationships are more valuable during times of hardship because they help individuals to cope with intra-group competition (van Schaik and van Noordwijk, 1989). In contrast, a negative relationship between network connectedness and the level of resource competition, as measured by group size, suggests competition rather than cooperation shapes sociality in wild chimpanzees (*Pan troglodytes*: Lehmann & Boesch, 2009). In sleepy lizards (*Tiliqua rugosa*), the number and strength of network connections does not change in response to changes in climate, although the nature of social connections differs with fewer inter-sexual associations in drier years (Godfrey et al., 2013). In contrast, the social networks of some populations do not appear to respond at all to changes in the physical environment. Although guppies (*Poecilia reticulata*) from areas with low levels of predation show more social mixing than their high-predation counterparts, no changes to social networks occur within populations following experimental manipulation of habitat complexity or predation risk (Edenbrow et al., 2011).

In addition to changes in the physical environment, network dynamics following changes in social factors, such as reproductive seasonality (Hamede et al., 2009; Brent et al., 2013b) and group composition, have revealed important information about social processes. For instance, network dynamics following the simulated, experimental, or natural loss of individuals from groups suggests that some individuals are more important to group cohesion than others (Lusseau, 2007; Manno, 2008; Kanngiesser et al., 2011) and can occupy specific social roles (Flack et al., 2005, 2006). Following experimental manipulation of the sex ratio of guppy groups, a breakdown in female-female associations in populations with a greater number of males, and hence a greater level of sexual harassment, suggests that repeated social interactions are

needed to establish individual recognition between group mates (Darden et al., 2009). Wild chacma baboon (*Papio ursinus*) females compensate for the death of close relative by broadening and strengthening their grooming networks (Engh et al., 2006), particularly by extending their social relationships to unrelated group mates. This apparent compensatory behavior suggests that social relationships are valuable to female baboons, and also provides preliminary evidence regarding the differential value of social relationships with kin compared to non-kin. Finally, changes to social networks have been observed in response to changes in the social hierarchy. The grooming networks of female chacma baboons were less diverse in the weeks following a period of instability in the alpha male position in their group (Widdig et al., 2006; Wittig et al., 2008b). Females who contracted their grooming networks the most showed a less dramatic rise in fecal glucocorticoid metabolite levels and returned to baseline levels more quickly. Taken together, these findings suggest that affiliative bonds with a small number of preferred partners help these animals to cope with social instability.

Network dynamics can occur not only in response to changes to the environment but can also precede or even provoke such changes. Understanding the links between network dynamics that occur in advance of shifts in the physical or social environment can therefore also have important implications for our understanding of social processes and relationships and may even allow scientists to predict the occurrence of major events. Instances where we might expect network dynamics to occur in advance of social or physical perturbations include: seasonally predictable changes in climate or resource abundance; the joining/splitting of subgroups in species with high levels of fission-fusion sociality (Sueur and Maire, 2014); large outbreaks of intra-group aggression; and the dispersal, death (i.e. in cases where death is preceded by a gradual decline in condition) or permanent eviction of group mates. However, few studies have

documented network dynamics prior to major events because the occurrence of these events can be difficult to anticipate, and studies of this nature often must rely on coincidental collection of behavioral data (Feldblum et al., 2018).

Here we evaluate network dynamics preceding the permanent mass eviction of females from a group of rhesus macaques (*Macaca mulatta*). Rhesus macaques, like many primates, live in social groups composed of multiple adult males and females (Thierry, 2007). Females are the philopatric sex and membership of females in rhesus macaque groups is “closed” (i.e. females do not disperse in/out of groups, they must be born into them). Nevertheless, rhesus macaque groups are characterized by a mixed relatedness structure, containing both related and unrelated females (Missakian, 1972; Brent et al., 2013b). Relationships are often the strongest and most stable between kin, but social bonds between unrelated females are also common (Cheney, 1992; Beisner et al., 2011b). In addition to high rates of affiliative interactions, social life in female rhesus macaques is characterized by high rates of aggression that is unidirectional (i.e. aggression is typically directed from high to low ranking animals) and that occurs within strict, linear, and relatively stable dominance hierarchies (Datta, 1988). Females inherit the rank immediately beneath their mother and thus closely related females tend to be of similar dominance rank (Missakian, 1972; Brent et al., 2013a). Permanent evictions of females have been documented in this species but are rare (Chepko-Sade and Sade, 1979b; Ehardt and Bernstein, 1986; Widdig et al., 2006). Because of the relatively stable social structure that characterizes female rhesus macaque life, it is reasonable to assume that social markers of instability would be detectable prior to a mass eviction but this has not yet been described.

The eviction that is the focus of this study occurred in a group of 55 adult females from three separate ancestral lines and resulted in the removal of the 13 highest ranking females. We

examined the aggression and grooming networks of all adult females during two periods preceding the eviction, the year immediately before the eviction (2011), and the year before that (2010). We determined whether network dynamics occurred in advance of the eviction by examining three aspects of social networks: i) the rate at which individuals engaged in social interactions, ii) individuals' choice of social partners and the nature of their interactions with those partners, and iii) the clustering of local subgroups.

Additionally, we examined network dynamics in the wake of the overthrow. Matrilineal overthrows are a dramatic reorganization of the social life of a group, and as such are anticipated to impart enduring consequences, but an eventual return to normality. Examining now the total group, that is, both males and females, we first calculate an individualized network-based measure for dominance instability (Fushing et al., 2011b; Vandeleest et al., 2016a) for the two years preceding (2010, 2011), the year of (2012), and two years that follow the overthrow (2013, 2014). We ask, iv) does the overthrow leave a visible signature in these interactions, and if so, what is the magnitude and duration of that signature? We also examine one phenotypic signals of psychosocial stress, the rate of self-directed behaviors (SDBs, self-scratching and -grooming: Schino et al., 1996; Castles et al., 1999; Troisi, 2002). With this, we address if, v) animals show visible signs of stress in the years spanning the overthrow.

## **METHODS**

### ***Study Population and Eviction Event***

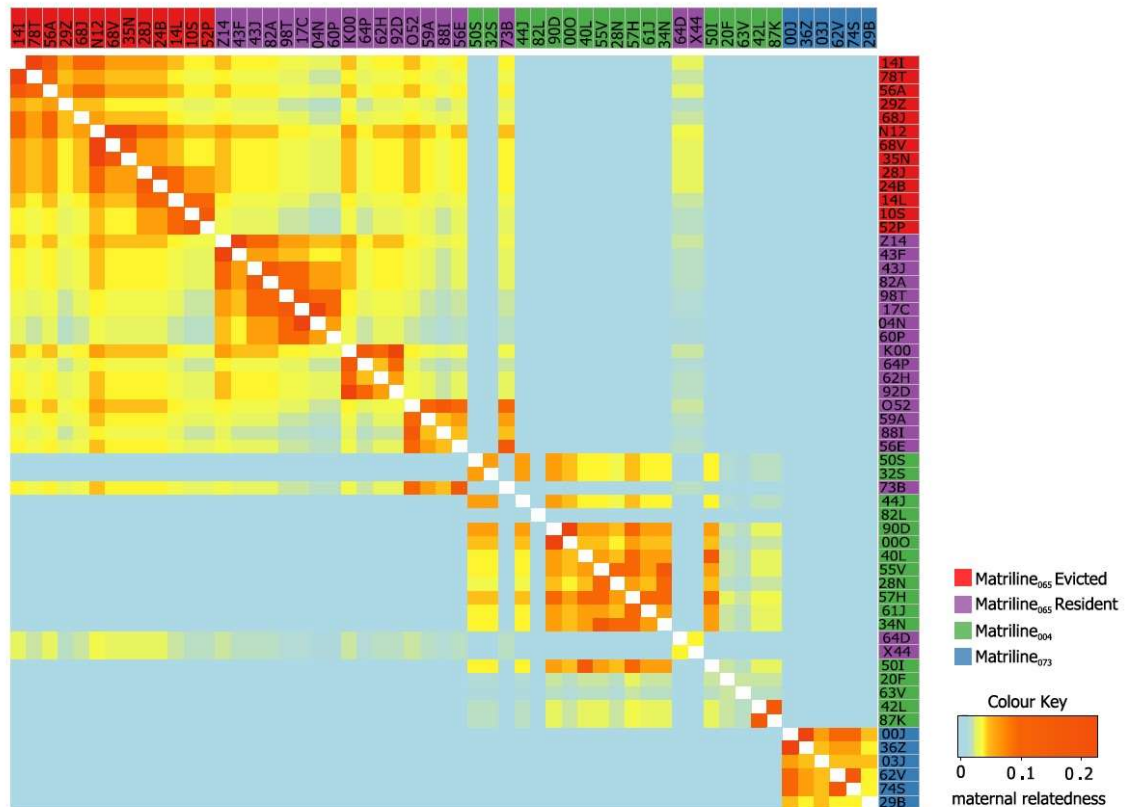
Our subjects were rhesus macaques living in the semi-free-ranging colony on Cayo Santiago Island, Puerto Rico (18°09 N, 65°44 W; Rawlings & Kessler, 1986). Monkeys are provisioned daily at this site with commercial feed and with water supplied *ad libitum*. There are no predators present. Population control takes the form of annual removal of mostly juveniles. Beyond these

measures, the monkeys are free to roam and to self-organize into groups and there is no medical intervention or contraceptive use.

We studied animals in a single social group ('F'), which at the time of study was the largest of the six groups on the island ( $n = 55$  adult females). Group F was made up of three separate female ancestral lines, or matriline, where all females in a given matriline are descendants of a single unique female, and where maternal relatedness between members of different matrilines is typically zero (Figure 1). The three matrilines were named after their founding females, 065, 004 and 073, who were first documented ranging together in group F over 50 years ago (unpublished, CPRC database), and varied in size ( $\text{Mat}_{065}$ ,  $n = 32$ ;  $\text{Mat}_{004}$ ,  $n = 17$ ;  $\text{Mat}_{073}$ ,  $n = 6$ ). Due to the linear nature of dominance hierarchies and the maternal inheritance of dominance rank, rhesus macaque matrilines can also generally be categorized according to rank:  $\text{Mat}_{065}$  contained the highest-ranking females, females from  $\text{Mat}_{004}$  were the next highest in rank (apart from three members of  $\text{Mat}_{065}$  that were lower in rank than some members of  $\text{Mat}_{004}$  - two of these females did not have many close relatives in the group and may have therefore lacked the social support needed to maintain high rank), and  $\text{Mat}_{073}$  contained the lowest ranking females (Figure 3.1).

At the beginning of 2012, we observed a sudden outbreak of aggression which resulted in the death of the alpha female and the permanent eviction of 12 of group F's highest ranking females (22% of all adult females; Figure 3.1). Although we could not collect systematic behavioral data during the aggressive outbreak, we opportunistically recorded cuts and wounds on the bodies of these members of  $\text{Mat}_{065}$ . The injuries sustained by the alpha female were especially severe and she died two weeks later, presumably from sepsis. The remaining 12 females began to range independently from the group along with their offspring and a few males. First, they ranged





**Figure 3.1 Maternal relatedness structure for the adult females in group F.** Female names are listed along the top and right-hand edge and are colored by matriline membership. Matriline 065 has been partitioned into females that were evicted and those that remained in the parent group ('resident') Females are ordered by descending dominance rank. Cells represent the maternal relatedness coefficient for each pair of individuals.

separately in two daughter groups then, approximately eight months later, as one consolidated group.

### **Data Collection**

As part of an unrelated study we collected behavioral data on the adult females in group F for two years prior to the eviction during two temporally similar periods: May-December 2010 and April-December 2011. These two periods were divided by a halt in behavioral data collection that takes place annually in the colony. All subjects were individually recognized and habituated

to observer presence. We collected a total of 843.70 hours of continuous data using 10-min focal animal samples with means (SD) per individual of 4.07 (0.39) and 5.02 (0.11) hours in 2010 and 2011, respectively. We balanced observations of individuals across time to control for within-daily as well as monthly temporal variation. We recorded all instances of aggression, submissive gestures, and grooming. We used agonistic win/loss interactions to construct dominance hierarchies for the females independently in each year, although female ranks were stable across years. We limited our analyses to females that were present for the entirety of the two years, which excluded a small number of females that died ( $n = 2$ ) as well as juvenile females that aged into our sample ( $n = 9$ ).

### ***Social Network Analysis***

We used social network analysis to explore network dynamics. Social network analysis is comprised of a suite of statistics that describe various levels of a network: individualized scores that describe properties of a node (e.g., a node's centrality), metrics that describe dyadic interactions (e.g., the probability of an edge between two individuals), and metrics that describe global network properties (e.g., size, shape, connectedness), making it apt at addressing the variation between individuals within a network and between networks at a subgroup, group, population, or species level (Krause et al., 2009; Brent, 2015)

To determine whether changes to networks occurred as the eviction approached, we compared the females' grooming and aggression networks from 2010 to those in 2011. We created one grooming and one aggression network for each year, resulting in four networks in total (Figure 2). Edges in these networks represented all observed grooming and aggressive interactions recorded within a given dyad. We treated networks as directed (i.e. the donor and recipients of an interaction are defined) and weighted (i.e. the rate at which a dyad interacted is represented

rather than the simple presence/absence of an interaction). For grooming networks, edges were weighted by the seconds per hour of grooming that took place within each dyad; for aggression networks, edges were weighted by the frequency of directed aggressive interactions per hour per dyad. Within years, our grooming and aggression networks were not significantly related to one another (2010: correlation coefficient = -0.025,  $p = 0.052$ ; 2011: correlation coefficient = 0.026,  $p = 0.086$ ) and thus we treat them separately in analyses.

### ***Changes in rates of social interaction***

We first determined whether the general tendency for all females to engage in social interactions changed as the eviction event approached by comparing grooming network and aggression network densities across years. We performed this analysis using the paired nodes density function in UCINET v6.588 (Borgatti et al., 2002) . Assessing changes to network density is an important first step before analyzing differences in network structure because apparent structural changes can be brought about by changes to density alone (Brent et al., 2013b) and so the impact of density on structural changes must be taken into account.

### ***Changes in the identity of social partners and the nature of social relationships***

We next explored whether the identity of social partners and/or the nature of social relationships changed in the year nearer to the eviction. Due to the maternal relatedness structure that underpins aggressive and affiliative interactions in this species (Missakian, 1972; Brent et al., 2013a) , we divided females according to their three ancestral matriline in order to explore changes in social partnerships that occurred within and between related partitions of females. We further divided matriline 065 into two partitions, 'Evicted' and 'Resident' to reflect the fact that the eviction was localized within this matriline and to allow us to examine any social changes that occurred between/amongst these females.

We evaluated the extent to which social interactions were directed within and between partitions in each study period using a joint-count analysis. This procedure starts by calculating the ratio of the observed edge weights that occurred within or between a particular partition(s) and the expected edge weights, which are generated from networks of similar size, density, and for which the edge weights are the median of the observed values. The ratio of observed to expected edge weights therefore describes the extent to which observed edge weights differ from those that would be observed if individuals interacted at random (that is, a model in which our chosen partitions were not meaningful). We then simulated 5000 random graphs in which the edges were reshuffled randomly between nodes (Erdős–Rényi networks). For each permuted network we calculated the observed to expected edge weight ratio. We evaluated the statistical significance of our observed edge weights by determining the proportion of permuted values that met or exceeded the observed value, a technique that is akin to traditional p-values (Croft, Madden, Franks, & James, 2011). We also compared the ratio of observed to expected edge weights across study periods in order to assess how partner choice changed as the eviction approached.

We predicted that the nature of aggressive interactions would change the year nearer to the eviction in a manner that would indicate instability in the dominance hierarchy. We therefore determined if there was greater tendency for females from lower ranking partitions to direct aggression at higher ranking partitions in the year closer to the eviction. We additionally explored changes to aggression within partitions, as instability could also be localized to more closely related females. For affiliative interactions, we predicted that grooming would be more focused onto related partners (i.e. within partitions) in the year nearer the eviction, as an additional indicator of social instability (Beisner et al., 2011b) and in accordance with previous

findings in Old World monkeys that suggest that kin-based relationships are more valuable during times of hardship (e.g., Engh et al., 2006).

### ***Changes to clustering of local networks***

We determined whether there were changes to the nature of local grooming networks across years. To do this, we compared the mean clustering coefficient for each partition in each study period. Clustering coefficient measures the degree to which an individual's social partners are connected to each other (Newman, 2002). The mean of this measure is therefore an indicator of the degree to which a partition is structured into tightly-knit cliques or clusters. We explored clustering coefficients of the grooming networks only due to the linear, non-triadic, nature of aggressive interactions in this species (Datta, 1988). We calculated a weighted version of clustering coefficient of using the *tnet* package in R (Opsahl and Panzarasa, 2009), which first necessitated converting our directed networks to undirected. We evaluated the statistical significance of observed clustering coefficients in two ways. First, we compared the clustering coefficient of a given partition within each study period to the clustering coefficient derived from a model of random association. To create random models, we generated 5000 (Erdős–Rényi graphs of similar size and density to the observed networks and calculated the mean weighted clustering coefficient in each partition for each permutation. We determined the proportion of these permuted values that met or exceeded observed values as a measure of statistical significance. In order to compare clustering coefficients across partitions, we performed a two-sample bootstrapping test. Here, we took the difference in mean clustering coefficients of the two partitions being compared (either the same partition across years, or different partitions within the same year). Then, we pooled together the clustering coefficients for each female in each partition. We resampled from this pool with replacement sets of equal size 5000 times and calculated the difference in the clustering coefficients that were generated

to create a null distribution. We calculated p-values as the proportion of differences in clustering coefficients between bootstrapped partitions that were more extreme than observed differences. To visualize differences in clustering across years, we generated 5000 random graphs in which the edge weights from a given partition were permuted but the positions of the edges held constant and created violin plots of the resulting values.

### ***Rank stability and phenotypic signals of psychosocial stress***

In the year of the overthrow, evicted females formed two temporary groups (Group NN and Group OO) in exile; 6 (46%) of these females would die soon in the weeks immediately following. For this reason, we chose not to examine the same matriline categories as we did in studying dynamic networks preceding the overthrow. Instead we examine total groups, consisting of all individuals, male and female, recorded in Group F during this time (2010 - 2014).

We first calculated rank stability using the *perc* package in R, which incorporates information from both direct and transitive aggressive interactions between individuals (Fushing et al., 2011a). When an individual's pair-wise interactions are more likely to be reciprocated (both directly and transitively through a third party), that individual is said to be more rank-unstable. In the past, rank-stability measures generated in a similar fashion were shown to exert an independent effect from rank on measures of physiological stress (Vandeleest et al., 2016a). We calculated this measure using matrices that contained all pair-wise instances of contact and non-contact aggression, displacement (whereby a dominant individual supplants and takes some resource from a subordinate), and threats (here defined as open-mouthed barking). Rank-stabilities were calculated independently for males and females. Next, we calculated the rates of a conspicuous behavioral signals of psychosocial stress, self-directed behaviors (SDBs). To do

this, we first parsed each 10m focal-follow into continuous periods in which the focal animal was recorded as resting, as outside the feeding corral, and as alone. For every individual in every study-year, we calculate the frequencies of these two behaviors and their rates.

## RESULTS

We found no evidence for changes between 2010 and 2011 in the overall rate of aggression (2010: 0.02, 2011: 0.02;  $t$ -stat=0.49;  $p$ =0.31) or grooming (2010: 1.20; 2011: 1.17;  $t$ -stat=0.13;  $p$ =0.43), as indicated by network densities. Any other structural differences in the observed networks (e.g., differences in clustering) cannot therefore be owed to differences in network density.

Aggressive interactions generally reflected the dominance hierarchy, with the majority of aggression emanating from higher ranking females and being directed at lower ranking females in both years (Table 3.1). However, changes from 2010 to 2011 in the extent to which aggression was directed up the hierarchy occurred and may suggest that there was instability in the dominance hierarchy that was largely localised to the 065 matriline. In particular, females from low-ranking matrilines 004 and 073 were more likely to give aggression to the Evicted females in 2011 compared to in 2010. Females from Mat<sub>004</sub> were also more likely to give aggression to the Resident females in 2011 compared to 2010 (Table 1). Although these increases represent only a small absolute number of aggressive interactions, reflecting the smaller number of females that belonged to the lower ranking matrilines (Figure 3.2), they are notable due to the typically unidirectional nature of aggression in rhesus macaques. The probability of aggressive interactions also increased amongst Evicted females from 2010 to 2011. However, there were decreases in the probability of aggression being directed from the Evicted females to the Resident females, and from the Resident females to the Evicted females.

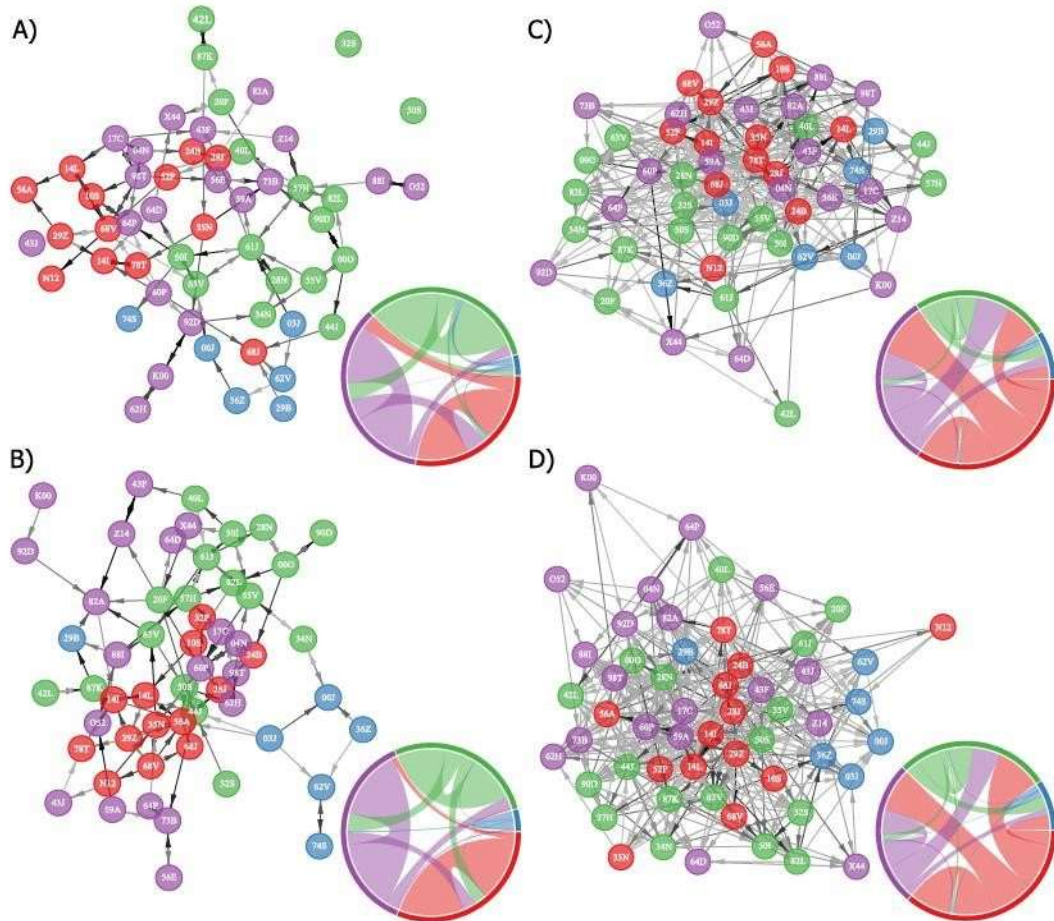
Donor	Recipient	Grooming Networks					
		2010			2011		
		Exp	Obs	Obs/ Exp (Pval)	Exp	Obs	Obs/ Exp (Pval)
Evicted	themselves	142	712	<b>5.02 (0.001)</b>	140	904	<b>6.45 (&lt;0.001)</b>
	Resident	207	201	0.96 (0.25)	205	69	<b>.34 (0.01)</b>
	Mat <sub>004</sub>	185	3	<b>0.02 (&lt;0.001)</b>	183	19	<b>0.10 (0.001)</b>
	Mat <sub>073</sub>	65	0	<b>0.00 (0.05)</b>	65	0	<b>0.00 (0.03)</b>
	Evicted	207	290	1.40 (0.48)	205	176	0.86 (0.17)
Resident	themselves	303	825	<b>2.73 (0.01)</b>	299	983	<b>3.29 (0.001)</b>
	Mat <sub>004</sub>	271	147	<b>0.54 (0.03)</b>	268	168	<b>0.63 (0.04)</b>
	Mat <sub>073</sub>	96	0	<b>0.00 (0.02)</b>	95	25	<b>0.27 (0.05)</b>
	Evicted	185	48	<b>0.26 (0.01)</b>	183	177	0.97 (0.24)
Mat <sub>004</sub>	Resident	271	244	0.90 (0.17)	268	245	0.91 (0.15)
	themselves	242	890	<b>3.67 (&lt;0.001)</b>	240	666	<b>2.78 (0.001)</b>
	Mat <sub>073</sub>	86	72	0.84 (0.32)	85	14	<b>0.17 (0.04)</b>
	Evicted	65	32	0.49 (0.22)	65	5	<b>0.08 (0.04)</b>
Mat <sub>073</sub>	Resident	96	0	<b>0.00 (0.01)</b>	95	21	<b>0.22 (0.04)</b>
	Mat <sub>004</sub>	86	68	0.79 (0.29)	85	7	<b>0.08 (0.02)</b>
	themselves	30	45	1.49 (0.30)	30	104	3.49 (0.08)
Aggression Networks							
		2010			2011		
		Exp	Obs	Obs/ Exp (Pval)	Exp	Obs	Obs/ Exp (Pval)
Evicted	themselves	2.43	8.00	<b>3.30 (&lt;0.001)</b>	2.18	8.37	<b>3.84 (&lt;0.001)</b>
	Resident	3.56	11.73	<b>3.29 (&lt;0.001)</b>	3.18	8.98	<b>2.82 (&lt;0.001)</b>
	Mat <sub>004</sub>	3.18	7.94	<b>2.50 (&lt;0.001)</b>	2.85	9.56	<b>3.35 (&lt;0.001)</b>
	Mat <sub>073</sub>	1.12	2.50	<b>2.23 (0.04)</b>	1.01	2.93	<b>2.92 (0.004)</b>
	Evicted	3.56	0.59	<b>0.17 (&lt;0.001)</b>	3.18	0.40	<b>0.13 (&lt;0.001)</b>
Resident	themselves	5.2	6.21	1.19 (0.38)	4.65	5.26	1.13 (0.19)
	Mat <sub>004</sub>	4.65	7.77	1.67 (0.08)	4.16	5.76	1.38 (0.48)
	Mat <sub>073</sub>	1.64	2.56	1.56 (0.27)	1.47	1.48	1.01 (0.15)
	Evicted	3.18	0.25	<b>0.08 (&lt;0.001)</b>	2.85	0.49	<b>0.17 (&lt;0.001)</b>
Mat <sub>004</sub>	Resident	4.65	1.13	<b>0.24 (&lt;0.001)</b>	4.16	1.2	<b>0.29 (&lt;0.001)</b>
	themselves	4.16	4.35	1.05 (0.19)	3.72	5.16	1.38 (0.37)
	Mat <sub>073</sub>	1.47	2.80	1.92 (0.09)	1.32	2.75	2.09 (0.08)
	Evicted	1.12	0.00	<b>0.00 (&lt;0.001)</b>	1.01	0.1	<b>0.10 (&lt;0.001)</b>
Mat <sub>073</sub>	Resident	1.64	0.12	<b>0.07 (&lt;0.001)</b>	1.47	0.1	<b>0.07 (&lt;0.001)</b>
	Mat <sub>004</sub>	1.47	0.12	<b>0.08 (&lt;0.001)</b>	1.32	0.1	<b>0.07 (&lt;0.001)</b>
	themselves	0.51	0.95	1.82 (0.14)	0.46	1.17	<b>2.52 (0.04)</b>

**Table 3.1 The magnitude of interactions within and between study partitions.** Observed and expected rates of grooming and aggression within and between females. The observed (Obs) and expected rates (Exp) of interaction, and the ratio of observed to expected for each network within and between the 4 partitions (Evicted, Resident, Mat<sub>004</sub>, and Mat<sub>073</sub>). Interactions emanate from "donors" and are received by "recipients." Pval is calculated as the proportion of simulated networks in which the Obs/Exp value exceeded or met the observed Obs/Exp value. Values in bold differed significantly from chance.



We found that, as expected, females were more likely to engage in grooming with members of their own partition. The Evicted, Resident, and Mat<sub>004</sub> females were more likely to groom members of their own partition compared to members of other partitions in both 2010 and 2011 (Table 3.1). This pattern was not significant for females from Mat<sub>073</sub>. Females also tended to groom females outside their own partition at rates either expected by chance or significantly lower than chance in both years. Yet there were notable differences in the identities of grooming partners both within and between partitions across years (Figure 3.2). For example, the tendency for females to groom members of their own partition increased from 2010 to 2011 for Evicted, Resident, and Mat<sub>004</sub> females, with the Evicted females showing the largest increase in within-partition grooming (2010: 5.02 *Obs/Exp*,  $p < 0.01$ ; 2011: 6.45,  $p < 0.01$ ). In addition, the amount of grooming that occurred between Evicted and Resident females did not differ from chance levels in 2010 but was smaller than expected in 2011 (2010: 0.96,  $p = 0.25$ ; 2011: 0.34,  $p = 0.01$ ). In other words, in the year nearer to the eviction, Evicted females were more likely to groom one another and less likely to groom the Resident members of their matriline.

The mean clustering coefficient of the grooming network of Evicted females was significantly greater than expected in 2011 but not in 2010 (Table 3.2). The mean clustering coefficient of no other partition differed from expected values in either year. In other words, the grooming relationships of Evicted females were more cliquish than expected based on random association in the year directly before their eviction, whereas no such differences were observed in the other partitions, including the Resident members of this matriline. The grooming relationships of the Evicted females were also significantly more clustered in 2011 than in 2010, and were significantly more clustered in 2011 than any other partition examined (Figure 3). Although there were small increases in clustering from 2010 to 2011 for the Resident and Mat<sub>004</sub> females,



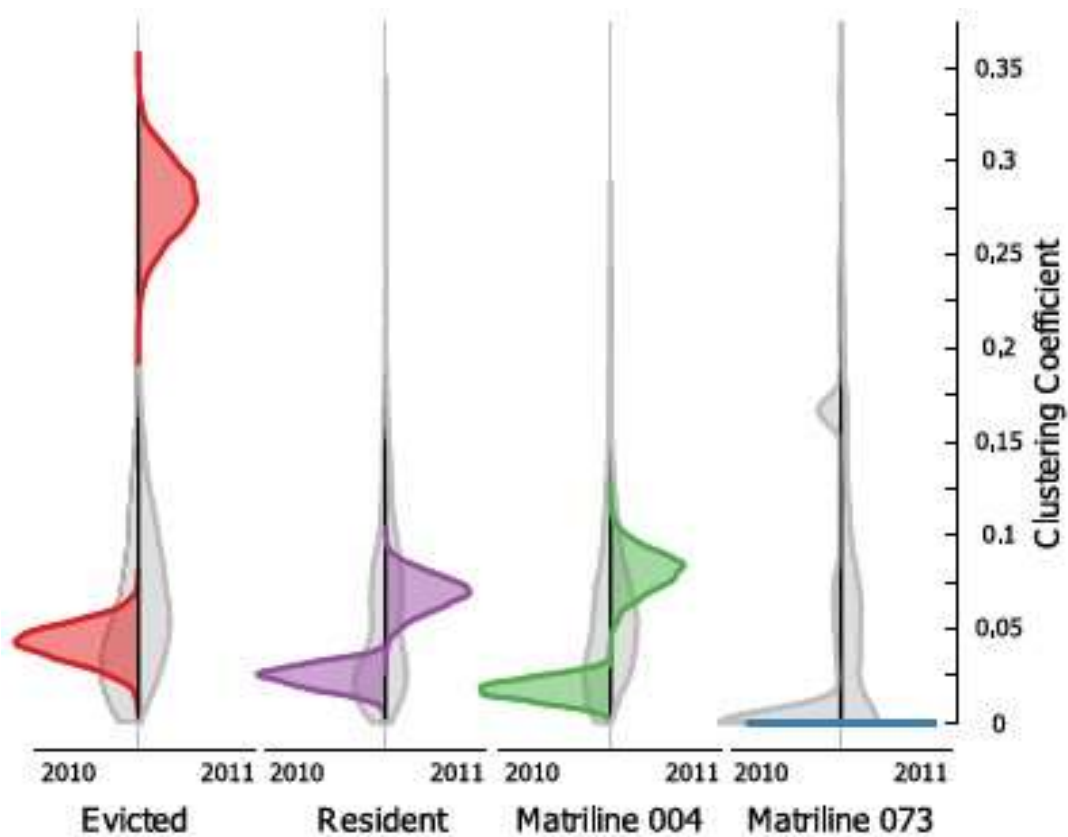
**Figure 3.2. Grooming and aggression networks in the years leading up to the overthrow.**

The grooming (A,B) and aggression (C, D) networks for 2010 (A,C) and 2011 (B,D). Node color represents partition membership where Evicted females are red, Resident females purple, Mat<sub>004</sub> females green and Mat<sub>073</sub> females blue. Color intensity of the edge arrows indicates the relative weight of the interaction, with darker edges indicating greater intensity. Each network is force-directed using the Fruchterman-Reingold algorithm. Inset chord diagrams: width of chords represents that summation of interactions emanating from a given partition to other partitions. Chords take the color of the partition from which interactions emanate.

this was only significant for the latter (Table 3.2). The clustering coefficient for Mat<sub>073</sub> was zero, as there were no closed triads within the network, thus no amount of edge-weight reshuffling could produce a result other than zero. We found relative similarities between our random graphs across years (Figure 3.3). Because changes in network densities were the central drivers

Matriline	Year	Observed Clustering Coefficient	Randomized Networks	Evicted		Resident		Mat <sub>004</sub>		Mat <sub>073</sub>	
				2010	2011	2010	2011	2010	2011	2010	2011
Evicted	2010	0.04	0.01 (0.49)		<b>0.23 (&lt;0.01)</b>	-0.01 (0.31)	-0.02 (0.23)	0.03 (0.08)	<b>0.05 (0.05)</b>	0.05 (0.09)	0.05 (0.09)
	2011	0.28	<b>0.21 (&lt;0.01)</b>			<b>0.24 (&lt;0.01)</b>	<b>0.21 (&lt;0.01)</b>	<b>0.26 (&lt;0.01)</b>	<b>0.18 (&lt;0.01)</b>	<b>0.28 (&lt;0.01)</b>	<b>0.28 (&lt;0.01)</b>
Resident	2010	0.02	0.02 (0.35)				0.03 (0.13)	0.02 (0.15)	<b>0.06 (0.03)</b>	0.04 (0.17)	0.04 (0.17)
	2011	0.07	0.001 (0.43)					<b>0.04 (0.01)</b>	0.03 (0.15)	<b>0.06 (0.02)</b>	<b>0.06 (0.02)</b>
Mat <sub>004</sub>	2010	0.02	0.03 (0.22)						<b>0.08 (&lt;0.01)</b>	0.02 (0.14)	0.02 (0.14)
	2011	0.08	0.02 (0.24)							<b>0.09 (0.01)</b>	<b>0.09 (0.01)</b>
Mat <sub>073</sub>	2010	0.00	0.04 (0.69)								0.00 (1.00)
	2011	0.00	0.06 (0.29)								

**Table 3.2 Significance testing of grooming network clustering coefficients.** P-values for the difference in observed and random networks are calculated as the proportion of random networks that produced values as extreme the observed value. P-values for the difference of observed values across partitions and study periods are based on a bootstrap twosample permutation tests. Values in bold differ significantly from chance.



**Figure 3.3 Mean clustering coefficients by partition.** Violin Plots showing estimates of the mean clustering coefficient for each partition in each study period. Grey plots how estimates for the given partition and year based on Erdős-Rényi random graphs. Colored densities represent mean clustering coefficients from 5000 permuted graphs in which we shuffled weights across edges while holding the positions of edges constant.

of differences between the random graphs, this further suggests that differences across time in our observed clustering coefficients were not driven by differences in density alone.

We see no significant change in rank-stability in Group F from 2010 to 2011 (Est. (SE): .007 (.01); p-value = .55; Table 3.3; Figure 3.4 Panel A). However, in 2012, there is a precipitous crash in these levels for both males and females (Est (SE): -.11 (.005); p-value <.001), which slowly return to pre-overthrow levels over the next two years (Est (SE): .13 (.005); p <.001). There was a significant increase in the resting rates of self-directed behaviors moving from 2010 to 2011

(Est. (SE): 13 (2.01; p-value < .001), and a significant drop moving from 2011 to 2012 (Est. (SE): -14.67 (2.21); p-value < .001; Table 3.3; Figure 3.4 Panel B). However, no trend was visible in the years following the overthrow.

Year	Rank Certainty		SDBs	
	Male	Female	Male	Female
2010	0.84	0.86	36.72	24.75
2011	0.85	0.88	51.2	37.3
2012	0.62	0.66	31.02	25.68
2013	0.75	0.85	32.72	22.87
2014	0.9	0.92	28.85	22.19

**Table 3.3 Average rank certainties, and average resting rates of self-directed behaviors for males and females by group and year.**

## DISCUSSION

The study of dynamic social networks is an area of rapidly growing research interest (Bode et al., 2011; Pinter-Wollman et al., 2014; Ilany et al., 2015). Although social networks appear to be able to flexibly respond to changes in the social and physical environment, whether changes to social networks also precede major events is less clear. Here we report network dynamics in advance of the mass eviction of members of the philopatric sex. Prior to the eviction, researchers present in the group reported no conspicuous signs of social instability. Therefore, the changes to the networks of these animals occurred in advance of a major event but were subtle and revealed only through subsequent analysis. Permanent evictions can have serious consequences for individuals; intragroup aggression prior to evictions can result in fatal injuries (Samuels and Henrickson, 1983b; Ehardt and Bernstein, 1986; Gyga et al., 1997; Oates-O'Brien et al., 2010), impacts to reproduction (Dettmer et al., 2015; Herrington et al., 2016), and exposure to predation (Krause & Ruxton, 2002). In the present study, rank-instability endured for two years following the overthrow. There is some evidence that reproductive competition

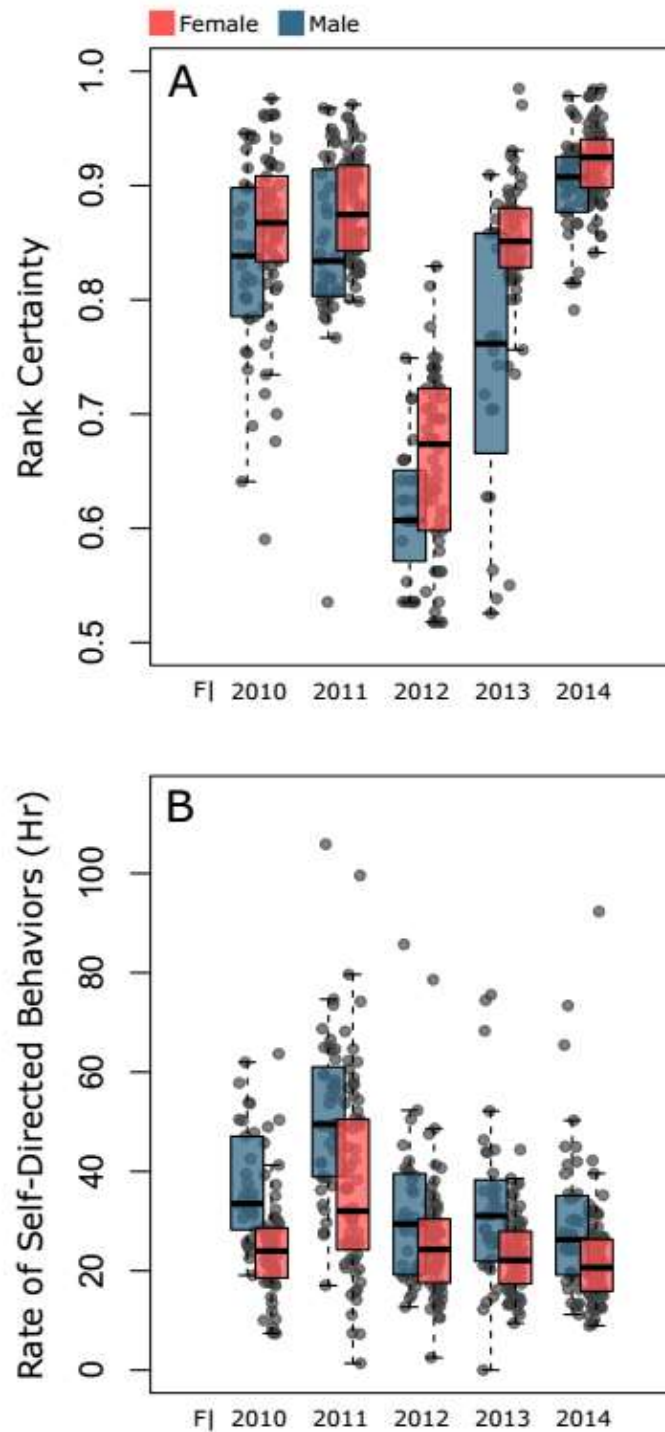


Figure 3.4 Box-plots of rank certainties (A) and the resting rates of self-directed behaviors (B) for males (blue) and females (red) by group and year.

the trigger for evictions in cooperative breeding species (Beisner et al., 2011a; Thompson et al., 2016), but it is unclear whether similar factors would be at play in a primate such as the rhesus macaque that has highly polygynous mating and only moderate levels of reproductive skew (Dubuc et al., 2014). Although we do not know whether there are causal links between changes to the social networks in this study and the eviction, a consistent patterning of network dynamics prior to evictions would nevertheless allow evictions to be predicted in future, which could have implications for the management of captive groups (Beisner et al., 2011b) and the design of naturalistic experimental studies.

Several theories have been put forward regarding the maintenance of group cohesion and the balance of competition and cooperation between unrelated group mates. For instance, group cohesion may be limited by the amount of time individuals have available to spend engaged in social interactions. This ‘time-constraints’ model predicts that groups break apart once individuals can no longer maintain or keep track of relationships with all other groups members (Dunbar, 1991, 1992). Prior to the mass eviction in this study, we did not detect any changes in the amount of time individuals dedicated to grooming or aggressive interactions, nor did we find any changes in our rank-stability measure. Although these animals are provisioned and may not easily suffer from restrictions in their daily time budgets, our results nonetheless suggest that the break down in group cohesion did not follow from reductions in social effort.

Group cohesion may depend not only on the amount of time individuals engage in social interactions but also on with whom they interact. For example, pay-to-stay mechanisms, whereby individuals ‘pay’ their group mates with affiliative interactions, have been proposed as a means to maintain groups of cooperative breeders with highly skewed reproductive success (Gaston, 1978; Johnstone and Cant, 1999; Bergmüller and Taborsky, 2005) as well as groups of

unrelated animals faced with intense between-group competition (Wrangham, 1980; van Schaik and van Noordwijk, 1989; Radford, 2008). In the latter instance, dominant animals are proposed to use social interactions, e.g., grooming, to establish alliances with their lower-ranking group mates in order to ensure they will help in contests with other groups (van Schaik and van Noordwijk, 1989; Cheney, 1992). A meta-analysis of data from cercopithecine primates suggests the link between grooming relationships, intra-group contest, and the maintenance of group cohesion is weak if non-existent (Cheney, 1992) (although see: Majolo, de Bortoli Vizioli, & Lehmann, 2016). In the present study, an increase in cliquishness in the local grooming networks of Evicted females, suggests that grooming relationships amongst kin and non-kin of divergent social status may indeed play a role in the cohesion of rhesus macaque groups. However, cause and consequence cannot be disentangled here and just as the reduced diversity of grooming relationships may have caused the eviction, the pending eviction may have resulted in the reduction of diversity in grooming relationships.

In the two years prior to the overthrow, there was a significant increase in the rates of self-directed behaviors in both males and females, further endorsing that, even though conspicuous markers of an impending overthrow were not apparent to human observers, this period was characterized by an increase in psychosocial stress. The years following the overthrow, however, were characterized by inconsistent and non-intuitive patterns in our psychosocial measures. Rank-stability, sensibly, showed its lowest point in the year of the overthrow, returning to prior levels gradually over the next two years. This pattern seems a sound confirmation of the overthrow as a destabilizing event, one engendering a lasting uncertainty in rank and thus greater reciprocity in aggressive interactions which, eventually, stabilize. However, this period was not characterized by changes in the rate of SDBs. Although impossible to assign an exact



mental state to this behavior, it may be the case that SDBs signal the anticipation of conflict, and that although some ambiguity in dominance rank lingers, most of that impending conflict was resolved by the eviction.

Changes to affiliative relationships leading up to a mass eviction also reveal more direct information about the patterns and processes that underpin social relationships in these animals. Biologists' understanding of the evolution of social bonds in animals has grown rapidly in recent years (Silk et al., 2009; Seyfarth and Cheney, 2012; Brent et al., 2013a; Chang et al., 2013; Archie et al., 2014). Affiliative tendencies have been shown to be heritable (Lea et al., 2010; Brent et al., 2013a, 2014b) and a positive association between affiliative relationships and proxies of fitness have been found in a small range of species, including baboons (Silk et al., 2009; Archie et al., 2014) and rhesus macaques (Brent et al., 2013a). Yet despite these advances, the adaptive functions of social bonds remains unclear (Brent et al., 2014a). A growing number of studies that have shown that affiliative social relationships between members of the philopatric sex are more flexible in nonhuman primates than traditionally believed (e.g., Barrett, Gaynor, & Henzi, 2002; Barrett & Henzi, 2002; Engh et al., 2006; Wittig et al., 2008). In accordance with this work, we found evidence for dynamic shifts in affiliative relationships in this study. Together, these findings may reflect the use of social relationships to cope with the vicissitudes of life such as death, disease, and shifts in social status, as well as other short-term social, environmental, and demographic events.

Our results may also hint that some social bonds are more valuable than others. Previous work has shown that instability in primate groups can be followed by shifts in social partners. Following the death of the alpha male in wild chimpanzees, individuals became more socially discriminant of grooming partners that failed to reciprocate (Kaburu and Newton-Fisher, 2013).

In cercopithecines, social relationships are most common amongst related females (Cheney, 1992). Relatedness may be a useful shorthand for reliable cooperative partners because of the ability to gain inclusive fitness benefits via these relationships. Female baboons focused their grooming networks onto close kin following instability in the male hierarchy (Widdig et al., 2006). In the current study, grooming relationships largely collapsed along kin-lines prior to the mass eviction, with Evicted females in particular focusing their relationships onto their closest kin; in times of social instability, affiliative relationships with non-relatives may become too risky for rhesus macaque females (but see Cheney et al., 2016). (Cheney et al., 2016)

The adaptive role of social relationships in variable contexts begs an understanding of how individuals of variable phenotypes integrate to form particular group dynamics. The stability of a group is not attributable to the phenotype of any one particular individual but it is likely nevertheless to impact upon individual fitness. Research in group-living species suggests that the interplay between group stability and individual fitness is complex (Wolf et al., 1998; Muir, 2005; Saltz, 2013). A more thorough understanding of how the metagenome (i.e. the influence of one individual's genotype and phenotype on another's) influences network dynamics will also be useful for behavioral ecologists approaching these questions.

## **CHAPTER 4**

### **AFFILIATIVE NETWORKS IN THE WAKE OF ENVIRONMENTAL DISASTER: HURRICANE MARIA AND THE CAYO SANTIAGO RHESUS MACAQUES**

#### **INTRODUCTION**

Multiple decades of human biomedical research have implicated social isolation in the development and severity of pathologies (Becofsky et al., 2015; Yang et al., 2016b), with its impact on mortality often exceeding that from tobacco and alcohol use (Holt-Lunstad et al., 2010). In nonhuman primates, social investment is a major contributor to genetic fitness (Sapolsky, 2004; Silk, 2007a): those with strong social bonds are often observed to live longer (Silk et al., 2010; Archie et al., 2014; Brent et al., 2017a) and secure greater reproductive success (Schülke et al., 2010; Brent et al., 2013a) than those without. These findings affirm social investment as a critical adaptation of the Order Primates.

Just how social bonds mechanically operate to produce these health and fitness outcomes remains a difficult question to answer. Their importance may be in their ability to mitigate the negative consequences of environmental instability. In humans, the presence of strong social support networks allay vulnerabilities to post-disaster stress disorders in a variety of circumstances, such as, to natural (Weems et al., 2007; Galea et al., 2008) and man-made (Cherry et al., 2015) disasters; to war (King et al., 1999) and terrorism (North et al., 2002; Otto et al., 2007; Neria et al., 2011). Social bonds in nonhuman primates also play a critical role in weathering destabilizing events. For example, following instability imparted by the death of the

alpha-male, female baboons (*P. hamadryas*) that were engaged to a reliable set of reciprocating partners showed attenuated rises in glucocorticoid levels and a faster return to baseline (Wittig et al., 2008a); a property that was also shown to improve stress levels during times of stability (Crockford et al., 2008). The mitigating effect of social support on the development of pathology in the context of instability is partly determined by underlying genetic background (Kaufman et al., 2004; Taylor et al., 2006; Reinelt et al., 2014), suggesting that this feature might potentially be shaped by natural selection.

Despite the clear adaptiveness of social bonds, individuals nevertheless show considerable variation in their propensity to invest into social relationships (Brent et al., 2017b). In organic, cooperative systems, individuals must strike a balance between investing into their immediate needs and investing in others, the latter being a riskier venture and one more likely to pay-off in the long-term (Krause and Ruxton, 2002). This is the central premise of the Prisoner's Dilemma model of cooperation (Axelrod, 1980; Nowak and Sigmund, 1993). In the context of environmental instability, this tradeoff can adopt a greater primacy. Humans are observed to shift their focus towards short-term goals if they feel their environment is unreliable (Griskevicius et al., 2011; Kidd et al., 2013). In the wake of the destruction of Cyclone Pam in 2015, Vanuatu residents who experienced high levels of property damage exhibited a decrease in their tendency to attend to the needs of others; conversely, if they themselves did not suffer such damage but were surrounded by those who did, this tendency increased (Vardy and Atkinson, 2019).

This tradeoff is also observed to operate within nonhuman primate groups. The reduction of a critical food source can introduce ambiguity in foraging times, which can demotivate individuals from investing in social bonds (Dunbar, 1991, 1992). Following the decimation of high-quality

food items following a hurricane, Spider monkeys (*A. geoffroyi*) were observed to more often range in smaller groups. Researchers argued that this change was an extension of this species' typical fission-fusion dynamics (Rodrigues, 2017), allowing them to more easily recover food in a drastically transformed landscape (Schaffner et al., 2012). Similar effects were observed in a population of howler monkeys (*A. palliata*) following human induced deforestation (Pavelka et al., 2003; Behie and Pavelka, 2005), as well as a decrease in the variability in the repertoire of their prosocial behaviors (Clarke et al., 2002). This tradeoff in the context of instability can also prompt more extreme divestments in prosociality. In a population of toque macaques (*M. sinica*), for example, population growth coupled with the loss of critical food sources following a cyclone prompted complete group dissolution: the fissioning of a single group into two daughter groups (Dittus, 1988). Thus, although there seems to be a clear adaptiveness of social bonds in the context of disaster, individuals nevertheless show differential investment in others in this context, seemingly owing to the tradeoff between such investments and their immediate needs.

In the present study, we examine the change in social relationships in the wake of environmental disaster in a population of semi free-ranging rhesus monkeys residing on Cayo Santiago island, Puerto Rico. On September 20<sup>th</sup>, 2017, Hurricane Maria made landfall onto Puerto Rico, then a category 4 storm with *ca.* 155 mph winds and caused widespread physical and environmental destruction. Although a contentious issue (Guha-Sapir and Checchi, 2018), multiple analyses place the human death toll of the Hurricane in the thousands (Kishore et al., 2018), making it among the most deadliest of storms on record. The island of Cayo Santiago was not exempt from this destruction. Following the hurricane, the island experienced near-complete deforestation, as well as fragmentation following the erosion of a critical, natural land bridge between island regions (Figure 4.1).



**Figure 4.1. Aerial photos of Cayo Santiago island, Puerto Rico of before Hurricane Maria (Left-Panel) and immediately after (Right-Panel).** The red circle in the right panel highlights the loss of a critical land-bridge connecting two regions of the island

To test the hypothesis that investments in social bonds represent an adaptive strategy to the stressors imparted by environmental disaster, we employ a long-term behavioral data set describing these animals, spanning many years prior to the hurricane to the year immediately afterward. We rely on the premise of behavioral flexibility (Strier, 2017), that individuals will facultatively and adaptively adjust their behavior in response to changing externalities.

Furthermore, we test the hypothesis that adjustments in prosocial tendencies will be predicated on variance in individual capital prior to the hurricane. In this population, most basic needs are uniformly met: animals are artificially provisioned with food and water and there is no natural predation. For these reasons, we predict that there will be a population-wide general increase in prosocial tendencies, both in their rate of occurrence and in the diversity of partners.

Furthermore, we predict that individuals in possession of the greater amounts of social capital prior to the hurricane will show the largest increases in prosocial tendencies moving from the pre-hurricane period to the post-disaster context

## METHODS

### *Study Population and Data Collection*

We examined a population of rhesus macaques living in a semi free-ranging colony on Cayo Santiago Island, Puerto Rico (18°09 N, 65°44 W; Rawlings & Kessler, 1986). The colony has been active and continuously monitored since 1938 following the transposition of animals originally captured in Asia. Cayo Santiago is managed by the Caribbean Primate Research Center (CPRC), which supplies commercial feed to the population daily and water *ad libitum*. Population management occurs in the form of annual removal of a set of individuals, mostly juveniles. There is no contraceptive use and no medical intervention. Animals are free to aggregate into social units as they would in totally free-ranging conditions. There are no natural predators on the island.

Prior to Hurricane Maria, behavioral data were collected under a 50+ ethogram using 10-minute focal follows on Teklogic Psion WorkAbout Pro handheld computers. All incidences of social interactions, both positive (*e.g.*, grooming and passive contact) and negative (*e.g.*, aggression, threats, submissions, and displacements) were recorded, along with their partner IDs, duration, and the initiator of the interaction. Additionally, we recorded all instances of two micro-movements, self-directed behaviors (self-scratching and -grooming) and vigilance (every turn of the head greater than 45°). At the 0-, 5-, and 10-minute marks of the focal follow, we performed instantaneous scan samples during which we recorded the state behavior of the subject (grooming, feeding, resting, and traveling), the identity of all individuals within two meters, and the respective state behaviors of those proximate individuals. Grooming is defined as the running of hands through a conspecifics fur for a duration lasting longer than five seconds. Feeding is further classified by the ingestion of one of three food types: the CPRC supplied food, plants, and water. Traveling is defined as a state of movement lasting longer than five seconds

and for a distance greater than 10 meters. Resting is the absence of these other behaviors. All focal follows were balanced across six time blocks to control for temporal variation.

After Hurricane Maria, the property damage to the surrounding community and the inconsistency of access to amenities such as electricity necessitated our adoption of a downgraded, paper-based means of recording data. In this context, we employed a reduced ethogram of only instantaneous scan samples, but collected them in an identical way to how they were collected prior to the hurricane. Scans in this context were collected far more frequently.

We examine three study groups with observations before and after Hurricane Maria. One of these groups, Group F, was particularly apropos to our analysis as it is the group for which we possess proximity scans as immediately after the Hurricane as possible, starting on October 26<sup>th</sup>, 2017. For a variety of circumstantial reasons, we were unable to collect a substantial number of data for this group in this timeframe, precluding our ability to draw strong conclusions from it. However, owing to their salience to the research question, we include a within-year comparison of proximity scans, before and after the hurricane, here for consideration. In the following year we were more able to regularly collect proximity scans for two groups, Groups KK and V, starting in January, 2018, and continuing until August: these data constitutes the bulk of our analysis. We used multiple years (KK: 2015, 2017; V: 2015, 2016, 2017) of observational data to characterize pre-Hurricane social behaviors. Across these groups, we collected 1593 hrs of observation in focal follows pre-hurricane, and 83,065 proximity scans both pre- and post-hurricane, across 459 unique individuals.

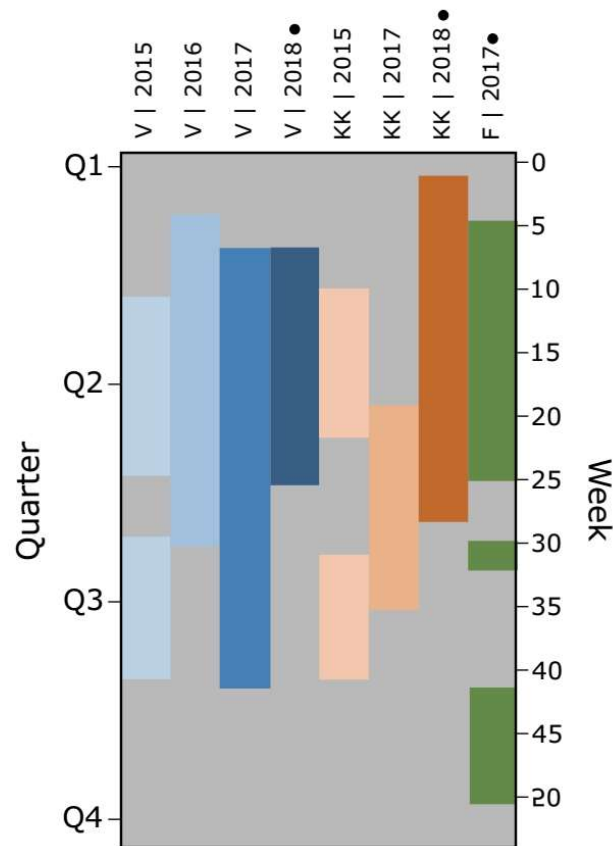


### ***Calculating Proximity and Grooming Interaction Rates***

The first goal of this analysis was to evaluate the influence of Hurricane Maria on two measures of sociality, the average number of proximity partners that an individual had per scan (henceforth the *proximity rate*) and the probability of being scanned in a state-of-grooming (the *grooming rate*). Although we have multiple years of representation of behaviors for these animals, the exact timings within-year of data collection are not exact matches (**Figure 4.2**). Rhesus monkeys show seasonal breeding and by extension seasonal variation in social behavior (Brent et al., 2013b). As we were concerned that the seasonality of these behaviors and the uneven representation of samples taken during specific seasons in a given year, we further parsed data sets by quarter of the year. For each quarter we calculated proximity and grooming rates for all individuals. We only included individuals who met a minimum of 15 scans to calculate these rates. Owing to a small number of individuals meeting this requirement, we omitted analysis for Q4 in both groups and Q3 of 2018 for Group V only. We use generalized linear mixed models (GLMMs; Bolker et al., 2009) to assess the significance of the hurricane, quarter, and interaction of the two on proximity and grooming rates. We controlled for demographic variables Age and Sex, included as fixed effects. Individual ID, group membership, and year are included as random effects.

### ***Calculating Partner Preferences***

To evaluate how the preferences for certain partner types have evolved after the hurricane, we used a permutation approach with subsamples from all proximity scans to generate bootstrapped social networks (1000 each) for Groups KK and V, pre- and post-hurricane, for each quarter. Again, we omitted Q4 quarter of all years and Q3 of Group V in 2018, owing to a lack of representation. Modeling social networks is highly sensitive to the methods of data



**Figure 4.2 The within-year timing of observations across groups.** Visual representation of the portion of a given year in which we have representative behavioral data for three groups, Group V (Blues), Group KK (Reds), and Group F (Green). Columns marked by a bullet point indicate periods that contain data taken after the hurricane.

collection (Castles et al., 2014), and for this reason much of our permutation procedure was designed to make as comparable as possible proximity scans collected under slightly different frameworks pre- and post-hurricane. Since preferences for certain partner types can be highly variable across the day (Sick et al., 2014), subsampled proximity scans were balanced across time blocks. Additionally, since provisioned food was no longer centralized within feeding corrals, we omitted the earliest time block when feeding occurred to remove this unstable source of variation. Finally, for pre-Hurricane networks, an additional component in our

subsampling procedure was added to avoid taking multiple scans from the same observation to obviate autocorrelation. All pre-hurricane years were consolidated into a singular hypothetical network containing individuals present at all intervals.

From these permuted networks, we calculated two network metrics and their standard errors. First, we calculated *network density*, the number of unique pair-wise connections observed. We also calculated *network equity*, how evenly social connections are distributed across individuals; lower values indicate more even distributions. To do this we employed gini coefficients, which yield a value between 0 and 1, with the former indicating totally homogenous distributions.

To assess changes in partner preferences, we used a joint-count procedure (Borgatti et al., 2002) to estimate the degree to which certain relationships occur within certain pair-wise categories. First, we examined the degree to which genetic relatedness structures these relationships. To calculate relatedness, we used census information of maternal assignment taken by the Caribbean Primate Research Center (CPRC) dating back to the sites' inception in 1938. Paternity assignment was based on 29 microsatellite markers for most animals born after 1985. Every subject in our sample has a known maternity; 97.4% have known paternity. We used the kinship2 package in R to calculate the pair-wise kin coefficient for all individuals within the sample (Sinnwell, Therneau, & Schaid, 2014). We examined permuted networks of females only. In this species, females are the philopatric sex and form the enduring social core of groups. Excluding males from this portion of the analysis prevented the dilution of the group coefficient of relatedness and the potential obfuscation of this relationship. We parse genetic relatedness into three categories: close-kin (kin coefficient  $> 0.25$ ), distant kin (KC:  $0.125-0.25$ ) and unrelated (KC  $< 0.125$ ). For each permuted network, we calculated the expected frequencies of proximity interactions that would occur in each of these categories if the distribution of connections was

random. For a given permuted network, we divided the observed frequencies of connections in each category by its expected value to generate a metric that conveys just how much their frequencies of occurrence exceed or fall short of chance.

We employed an identical procedure with full permuted networks to examine the degree to which proximity interactions occurred in same- or opposite-sex pairs. Furthermore, we log transformed all metrics generated by the joint-count procedure to make more comparable instances for which observed values fell short of expectation and when they exceeded it. To compare distributions of these network metrics for pre- and post-hurricane networks, we calculated and took as a measure of statistical significance their degree of overlap.

#### ***Factors that predict changes in social rates from pre- to post-hurricane***

We examined several social dimensions of 2017 social networks in Groups KK and V. First, we calculated *dominance rank* using the *perc* package in R (Fushing et al., 2011a). In brief, this package employs a procedure that incorporates information from both direct and indirect dominance interactions between individuals to create the linear dominance hierarchy that maximizes information flow. This procedure was employed on interaction matrices consisting of four behaviors: contact aggression, non-contact aggression (*e.g.*, chases), displacements, and threats. Second, this procedure also provided a singular metric (0.5 – 1.0) of *rank stability*, which measures the degree of reciprocity that exists in an individual's direct and indirect dominance interactions; individuals of rank-stability closer to 1 see their dominance interactions less likely to be reciprocated. We performed this analysis independently for males and females. Third, to assess aggression more generally, we also created adjacency matrices comprised of the directional, pair-wise rates of contact and non-contact (frequency/hr). We examined aggression *in-* and *out-strength*, the amount of aggression individuals received and emanated, respectively.

Finally, to assess prosociality, we created adjacency matrices comprised of directional, pair-wise grooming interactions (s/hr of observation). We examined grooming network *in- and out-strength*, which measures the amount of grooming that an individual receives and gives respectively.

As an additional test to evaluate the relationship between prior social capital and the magnitude of change in the rate of interactions, we also examined two conspicuous behavioral signals previously shown to index social capital: self-directed behaviors (SDBs) and vigilance. SDBs (self-scratching and -grooming) indicate sympathetic nervous system activation and have traditionally been taken as a measure of stress (Maestriperi et al., 1992; Troisi, 2002). Vigilance (here, operationalized as movements of the head greater than 45°) measures the degree to which an individual invests in social monitoring. Both measures have been found to increase among individuals with low social capital. In brief, we calculated the so-called *resting rates* of these behavior: that is, their frequency per hour of observation in which the focal individual was observed resting, alone, and outside the feeding corral. The significance of these variables was investigated in the context of three generalized linear models. The first included all social network variables as fixed effects, whereas the second and third included only the resting-rates of SDBs and vigilances, respectively. All models also included *Group Membership* as a random effect.

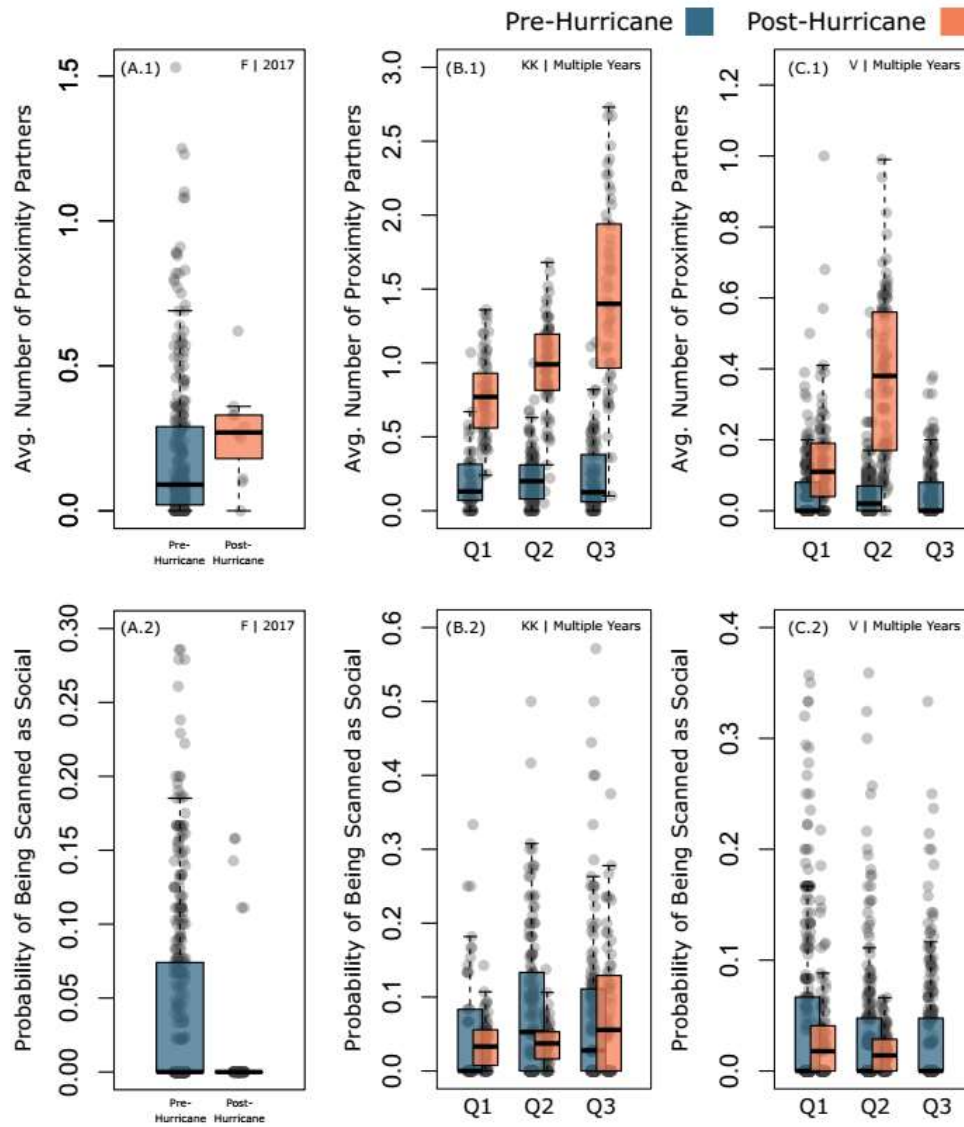
## RESULTS

### *Changes to Proximity and Grooming Rates*

We observed considerably large increases in individual proximity rates in the post-hurricane compared to the pre-hurricane samples; for groups KK and V this increase was statistically significant (Table 4.1; Figure 4.3, Top Row). In any given year, regardless of hurricane status,

Group	Fixed Effects	Proximity Rate			Grooming Rate		
		Est (SE)	Chisq	P-value	Est (SE)	Chisq	P-value
Group F	Sex	.07 (.03)	4.57	<b>0.03</b>	-1.33E-02 (8.91E-03)	2.22	0.14
	Age	-.001 (.003)	0.37	0.54	-7.28E-04 (8.81E-04)	0.68	0.41
	Hurricane	.08 (.08)	1.04	0.31	-1.31E-02 (2.27E-02)	0.34	0.56
Group KK	Sex	.24 (.04)	32.59	<b>&lt;.001</b>	1.3E-02 (6.87E-03)	3.59	<u>0.06</u>
	Age	.01 (.004)	6.28	<b>0.01</b>	-7.75E-06 (8.33E-04)	.0001	0.99
	Hurricane	.2 (.12)	101.85	<b>&lt;.001</b>	5.64E-02 (4.01E-02)	0.16	0.69
	Quarter	.01 (.02)	68.71	<b>&lt;.001</b>	2.82E-03 (5.52E-03)	2.93	<u>0.09</u>
	Qua*Hur	.33 (.03)	126.247	<b>&lt;.001</b>	2.04E-02 (8.05E-03)	6.44	<b>0.01</b>
Group V	Sex	.07 (.01)	24.69	<b>&lt;.001</b>	2.21E-02 (4.61E-03)	22.98	<b>&lt;.001</b>
	Age	.003 (.001)	6.9	<b>0.009</b>	-3.05E-04 (5.04E-04)	0.37	0.54
	Hurricane	.17 (.02)	138.55	<b>&lt;.001</b>	1.41E-02 (1.38E-02)	10.88	<b>&lt;.001</b>
	Quarter	.001 (.004)	27.81	<b>&lt;.001</b>	-6.89E-03 (2.08E-03)	12.01	<b>0.005</b>
	Qua*Hur	0.26	355.18	<b>&lt;.001</b>	-1.12E-03 (8.16E-03)	0.02	0.89

**Table 4.1 The impact of Hurricane Maria and season on the proximity and grooming rates.** We report the results of generalized linear mixed models to assess the impact of post-hurricane status, quarter (season), and the interaction thereof on individual proximity and grooming rates. Values in bold indicate relationships of statistical significance; underlined values indicate strongly trending relationships.



**Figure 4.3 Pre- and post-hurricane proximity (1) and grooming rate (2) for Group F (A), Group V (B) and Group KK (C).** Boxplots summarize individualized proximity and grooming rates pre- (blue) and post-hurricane (orange) for three groups (F, KK, and V), further parsed, when possible by quarter. Pre-hurricane boxplots for Groups KK and V summarize multiple years of data collection.

there was a general trend of increasing proximity rates as the year progresses from the mating season (Q1) into the birthing season (Q3). However, for groups KK and V, this rate of increase was accelerated in the post-hurricane samples.

The pattern of individual grooming rates was less clear. For Group V only, there was a small, statistically significant increase in the grooming rates post-hurricane (Table 4.1; Figure 4.3, Bottom Row). There were also significant main effects of quarter on social rates, but in ostensibly opposite directions for Group KK and V, which showed positive and negative correlations respectively. Finally, there was a significant interaction effect for post-hurricane status and quarter for Group KK only, in that there was a steeper increase in the grooming rates in the post-hurricane period as the year progresses. As anticipated, females across all study groups showed significantly greater proximity rates than males; for the grooming rates, this was significant for both Group KK and Group V. The proximity rates were also observed to increase with age.

### ***Changes in Partner Preferences***

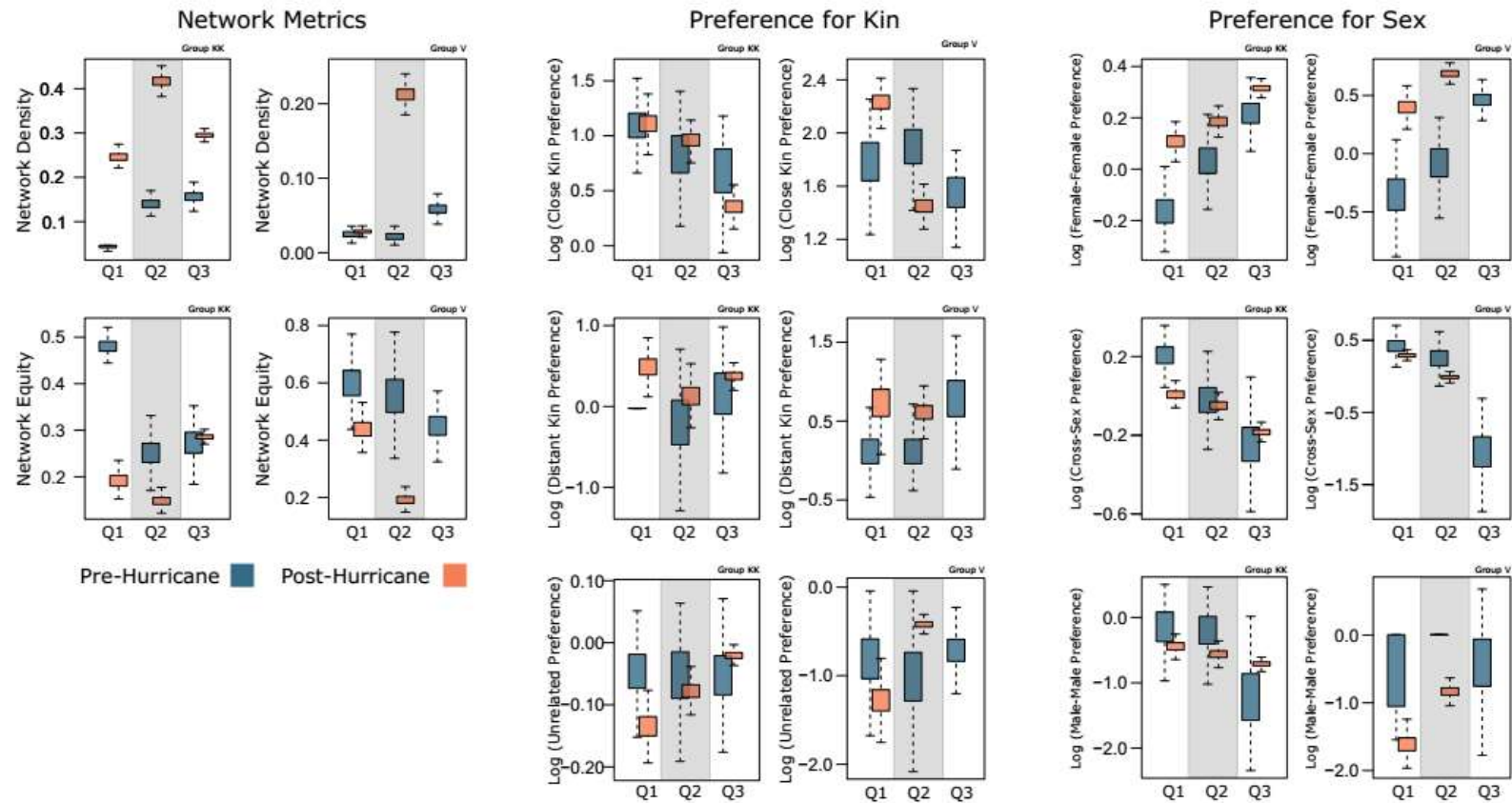
Both Groups KK and V showed general trends towards greater network density and greater network equity. In Group KK for all quarters, there was a significant increase in network density compared to pre-hurricane networks of the same quarter (Table 4.2; Figure 4.4, leftmost plots); for Group V, this was significant only in Q2. Both Groups KK and V in Q1 and Q2 of the post-hurricane year showed a more egalitarian distribution of pair-wise proximity interactions across individuals.

As anticipated, we observed strong evidence that females generally favored close-kin as proximity partners, and actively avoided unrelated females (Figure 4.4, center plots). Group KK



Study Group	Study Period	Quarter	Network Statistics				Preference for Kin				Preference for Sex						
			Density	p-value	Equity	p-value	Close Kin	p-value	Distant Kin	p-value	Unrelated	Fem Fem	p-value	Fem Mal	p-value	Mal Mal	p-value
Group KK	Pre-Hurricane	Q1	.04 (1.23E-05)		.47 (3.35E-04)		1.09 (.03)		Undef		-.04 (.002)	-.16 (.004)		.2 (.004)		-.13 (.13)	
		Q2	.14 (1.70E-04)		.25 (9.35E-04)		.84 (.06)		-.15 (.28)		-.05 (.002)	.04 (.005)		-.02 (.01)		-.2 (.12)	
		Q3	.16 (1.93E-04)		.27 (.001)		.7 (.09)		.18 (.15)		.05 (.002)	.21 (.004)		-.23 (.02)		-1.26 (.26)	
	Post-Hurricane	Q1	.25 (1.19E-04)	<.001	.19 (2.85E-04)	<.001	1.12 (.01)	.64	.49 (.02)	<.001	-.13 (5.73E-04)	.11 (.001)	<.01	.01 (8.34E-04)	.03	-.44 (.006)	0.21
		Q2	.42 (1.68E-04)	<.001	.15 (1.31E-04)	.01	.96 (.006)	.35	.13 (.02)	.39	-.08 (2.43E-04)	.19 (5.91E-04)	.06	-.05 (6.77E-04)	.34	-.56 (.006)	0.17
		Q3	.29 (3.69E-05)	<.001	.29 (4.10E-05)	.25	.36 (.006)	.2	.38 (.005)	.25	-.02 (5.55E-05)	.32 (2.15E-04)	.11	-.18 (3.94E-04)	.25	-.71 (.002)	0.09
Group V	Pre-Hurricane	Q1	.03 (2.46E-05)		.59 (.004)		1.77 (.06)		-.14 (.17)		-.76 (.15)	-.33 (.04)		.42 (.01)		Undef	
		Q2	.02 (3.06E-05)		.55 (.006)		1.93 (.04)		.27 (.15)		-1.02 (.18)	-.07 (.04)		.25 (.03)		Undef	
		Q3	.06 (6.68E-05)		.45 (.002)		1.56 (.03)		.81 (.15)		-.7 (.04)	.47 (.005)		-1.02 (.13)		-.37 (.27)	
	Post-Hurricane	Q1	.03 (8.42E-06)	.42	.43 (.001)	.07	2.24 (.005)	.06	.74 (.1)	.22	-1.29 (.04)	.4 (.005)	<.001	.29 (.001)	.2	-1.62 (.02)	0.1
		Q2	.21 (1.04E-04)	<.001	.19 (3.22E-04)	<.001	1.45 (.004)	0.08	.61 (.02)	.17	-.42 (.002)	.69 (.002)	<.001	-.01 (9.52E-04)	.1	-.83 (.005)	0.06
		Q3															

**Table 4.2 Network permutation statistics for global network properties and joint-count procedures.** We report the median and variance of network statistic distributions generated from our subsampling, permutation procedure. The degree of overlap of distributions between pre- and post-hurricane is reported adjacent to the post-hurricane values; taken as p-values, significant differences are reported in bold. Strongly trending differences are underlined. For the joint-count procedures (preference for kin and preference for sex) we report log transformed values to ease interpretation.



**FIGURE 4.4 Network permutation distributions for global network properties and joint-count procedures.** We draw boxplots to capture permuted proximity network statistic distributions for pre- (blue) and post-hurricane (orange) study periods.

showed no significant differences in their preferences for closely related, distantly related, or unrelated individuals in the post-hurricane sample. In Group V, however, we observed strongly trending differences in the preferences for close-kin, with greater preferences in Q1 and lower preferences in Q2 of the post-hurricane networks compared to pre-hurricane networks. In both groups, there was a general decline in preferences for close-kin. Regarding preferences for unrelated individuals, we observed an increase in preference for unrelated individuals in the post-hurricane networks, a trend that was not visible in the pre-hurricane networks.

As anticipated, individuals within both pre- and post-hurricane networks showed the greatest preference for opposite sex pairs in Q1, which corresponds to the mating season; a preference that declined as a given year progresses (Figure 4.4, rightmost plots). We found no difference in the degree of preference for opposite sex individuals in the pre- and post-hurricane networks. In both study groups, there was either a statistically significant or strongly trending increase in the preference that females had for other females. No corresponding pattern was found with males, although, in some instances the extreme, infrequency of observing such interactions precluded our ability to more accurately test this question.

#### ***Phenotypes that predict the magnitude of change of these rates***

We observed that the change in individual proximity rates from pre- to post-hurricane was highly predicted by indices of social capital. Individuals that were female, older, of high rank, high rank stability, and received more grooming from others show the largest increases in proximity rate in the post-hurricane period (Figure 4.5, leftmost columns; Table 4.3).

Furthermore, individuals in the pre-hurricane period that were hypovigilant (that is, had less need to invest in social monitoring) and showed lower rates of SDBs (were less stressed) also

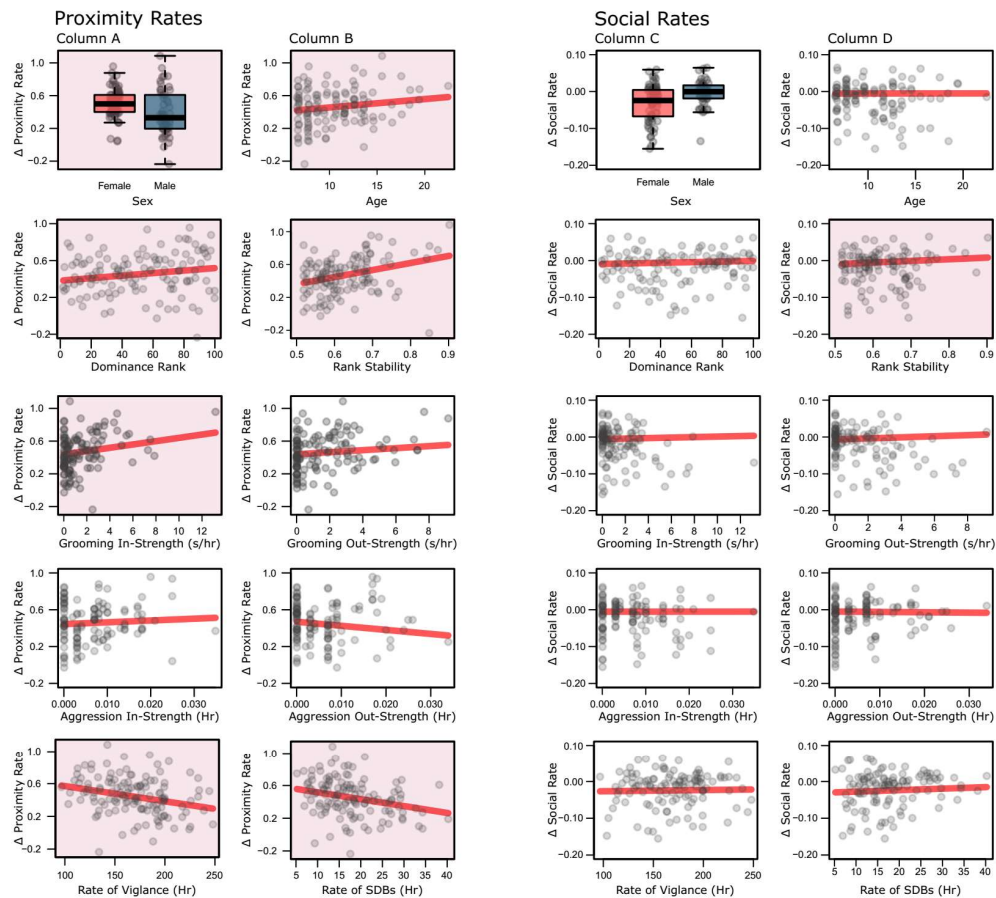
showed the highest increases. These findings did not translate into grooming rates. Here, we found a trending, but non-significant effect from rank stability, in a pattern that mirrored its relationship with the proximity rate.

## **DISCUSSION**

In this study, we have attempted to examine the ways in which the affiliative relationships of a semi free-ranging population of rhesus monkeys transform in the wake of environmental disaster. We find strong evidence that individuals spend significantly more time near others in this considerably degraded landscape, consistent with the hypothesis that social relationships serve an adaptive function during instability. In support of this hypothesis, we find evidence in one of our study groups that individuals invest more in social bonds by way of grooming while in that vicinity. We find these adjustments to social behavior were not instantaneous following the hurricane, but instead developed gradually during the following year. Over time, we observed increasing proximity rates, increasing frequencies of unique pairings of individuals, and increasing egalitarianism in the distribution of relations, so that individuals that were previously isolated in pre-hurricane networks showed greater involvement after the hurricane. In the post-hurricane year, females show an increased preference for other females of their groups; preferences that exceeded their levels in the pre-hurricane period. Concomitantly, females also show less avoidance of unrelated females. Finally, although the observed increase in proximity rates is exhibited population-wide, there is considerable inter-individual variation in the magnitude of this change. We find that individuals in possession of high levels of social capital in the year prior to the hurricane showed the largest increases in proximity rates, consistent with the hypothesis that prosocial adjustments in the presence of instability are predicated on an individual's prior security. Together, we take these findings as strong evidence for the flexibility

Fixed Effects	Change in Proximity Rate			Change in Grooming Rate		
	Est (SE)	Chisq	P-value	Est (SE)	Chisq	P-value
Sex	-0.1 (.04)	5.713	<b>0.02</b>	-5.71E-03 (4.03E-03)	2.0034	0.15695
Age	.01 (.01)	3.66	<u>0.06</u>	2.17E-05 (5.14E-04)	0.0018	0.96637
Rank	.001 (.001)	3.7	<b>0.05</b>	8.56E-05 (6.85E-05)	1.5608	0.21155
Rank Stability	.86 (.25)	12.2	<b>&lt;.001</b>	4.45E-02 (2.51E-02)	3.1565	<u>0.07563</u>
Grooming In-Strength	.02 (.01)	3.73	<b>0.05</b>	6.29E-04 (1.02E-03)	0.3842	0.53534
Grooming Out-Strength	.01 (.01)	1.34	0.25	1.49E-03 (1.10E-03)	1.8399	0.17496
Aggression In-Strength	1.97 (2.74)	0.52	0.47	3.88E-03 (2.62E-01)	0.0002	0.9882
Aggression Out-Strength	-4.41 (3.13)	1.98	0.16	-8.45E-02 (2.98E-01)	0.0803	0.77686
Value in 2017	-0.45 (.19)	5.9	<b>0.02</b>	-9.32E-01 (4.27E-02)	476.0792	<b>&lt;.001</b>
Vigilance	-0.0019 (.0006)	10.984	<b>&lt;.001</b>	2.87E-05 (1.21E-04)	0.056	0.81
Self-Directed Behaviors	-.008 (.003)	9.86	<b>&lt;.01</b>	4.12E-04 (5.72E-04)	0.52	0.47

**Table 4.3 The relationships between pre-hurricane phenotypes and the magnitude of increase in prosociality.** All social variables were considered in the context of a singular generalized linear mixed model as fixed effects. The rates of vigilance and self-directed behaviors were examined exclusively within their own models. Significant predictors are highlighted in bold; strongly trending values are underlined.



**Figure 4.5 Indices of social capital and their relationship to individual changes in proximity and grooming rates.** Significant predictors of the magnitude of change in proximity rate (leftmost columns) and grooming rate (rightmost columns). Lines are the partial regressions following their respective models. Plots with highlighted backgrounds indicate relationships of statistical significance of social relations, and the potential for environmental disaster to push individuals towards prosociality.

Our observation of increased proximity rates is robust across the two study groups. Our observation of increased grooming rates is less so, with visibility in only one of our study groups. Proximity is often used as a proxy for other forms of interaction, including grooming relationships (Farine, 2015), although they are not synonymous. Being drawn into close

proximity to others, especially unfamiliar conspecifics, is expected to be stressful *per se*.

Grooming can be exchanged for tolerance of others (Henzi and Barrett, 1999); elsewhere individuals have been seen using grooming as an active strategy to mitigate the stress imparted by close-quarters (Seres et al., 2001; Snyder-Mackler et al., 2016). Consequently, our discovery of grooming increase in only one study group should invite increased caution in interpretation. This heterogeneity between groups might be owed to small effects and inadequate sample sizes. However, there are also considerable differences in the social styles of Group KK and V. Group V ranges alone on “small cayo;” a region of the island that was severed from the island at large after the hurricane, making it the most reclusive group on the island. Furthermore, Group V has for many years the unique property of being the only group on the island in which the number of adult males exceeds the number of adult females. Colloquially, this pattern had been interpreted as Group V serving as a repository for males that are not, or unwilling to remain, competitive. This has yielded a group with a considerably less despotic social style. It may be these specific lineaments of Group V that allow grooming as a mechanism for mediating stress to figure more prominently.

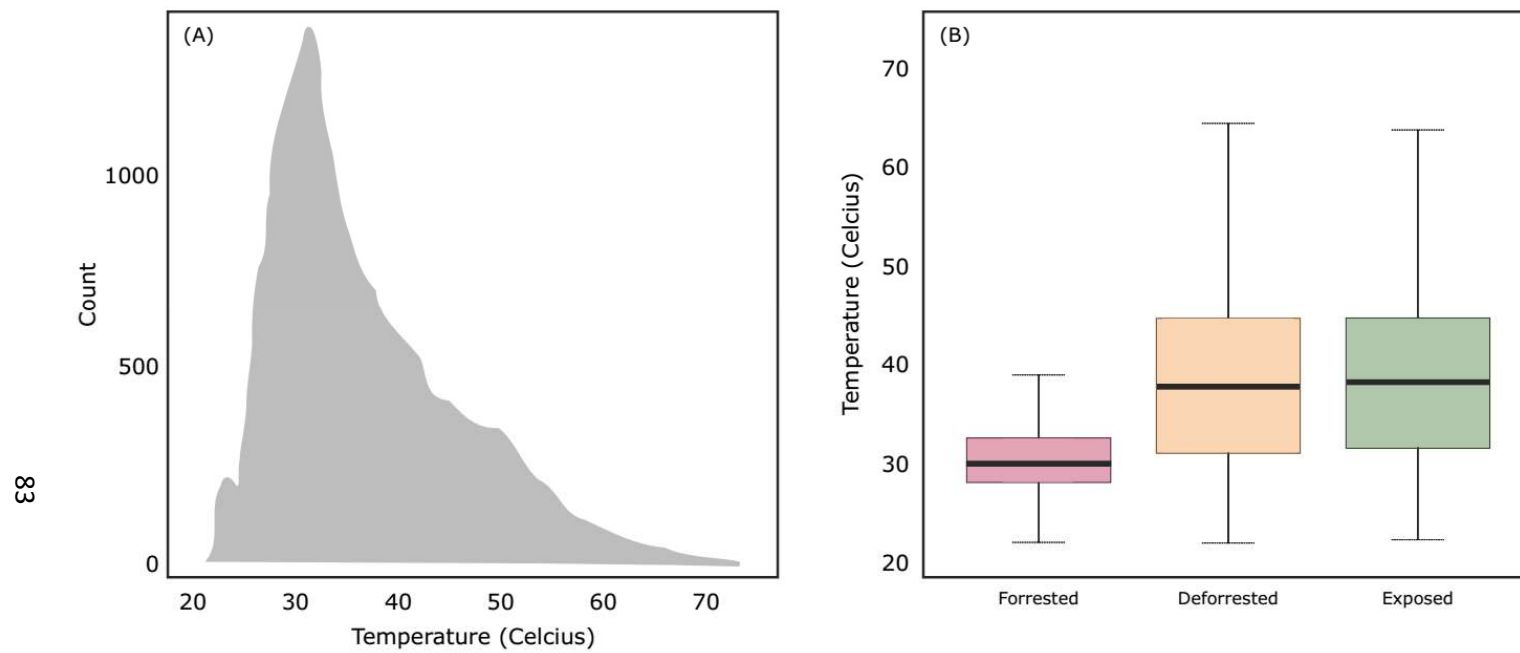
We observe strong evidence that these changes in social rates were not experienced uniformly by the population. Instead, individuals with secure social positions prior to the hurricane show the largest increases in prosociality. This finding is consistent with the hypothesis that investments in sociality are contingent on the ability of individuals to meet their more immediate needs. On Cayo Santiago island, food and water is artificially provisioned, and there is no natural source of predation; the largest and most consistent source of threat is from conspecifics. In this environment, individuals who yield high levels of social capital, that is, are of high social standing, receive friendly attention from others, and are stable in their dominance

position, hence possess the most ground to invest in social relationships during periods of instability.

Although our findings are consistent with the hypothesis that individuals become increasingly prosocial as a means of mitigating the stress of environmental disaster, a second, non-mutually exclusive hypothesis regarding such changes as benign manifestations of the distribution of resources. Following Hurricane Maria, Cayo Santiago island was nearly completely deforested. Rhesus monkeys, as a semi-terrestrial primate, frequently utilize the coverage provided by greenery, both as a means of avoiding predator detection and as a means of temperature regulation. Temperatures are considerably high in the Caribbean (Figure 4.5 Panel A), and foliage provides significant protection from them (Figure 4.5 Panel B). Thus, the increasing proximity rates observed in this study may, in fact, just be the result of individuals conglomerating around this now precious resource. Similar conglomerations have been observed in cercopithecine primates around rare food items (Sugiura et al., 2011). This observation invites reconceptualization of our interpretation of the heterogeneity across individuals in the magnitude of increase in prosocial measures. In this other conception, individuals of high social standing prior to the hurricane, that is, those who possess the widest pool of potential partners, are more likely to see that pool be utilized in the context of patchier resource distribution.

However, should resource distribution, and not stress management, be the primary explanation for adjustments in prosocial behavior, it nevertheless represents a notable finding regarding the malleability of these relationships. Prior to the hurricane, the abundance of leaf coverage allows individuals to harbor discriminating criterion in their partner choice. Now, to recover that resource, individuals must relax their criteria and show more tolerance for more frequent





**Figure 4.6 The distribution of daily average temperature (°C; Panel A) and the influence of greenery on temperature (Panel B).**

proximity to others, especially with unrelated individuals. As a more generalized phenomenon in both humans and nonhuman primates, disaster can expose relationships otherwise unobservable during times of stability (Molotch, 1970; Torry et al., 1979; Bond, 2013).

A critical thread of research in primate conservation studies is survival in human transformed landscapes. In the context of anthropogenic global warming, it is becoming increasingly difficult to say that any organism is spared from human encroachment (Lewis and Maslin, 2015). In the Anthropocene, living in human transformed landscapes, for example, those subject to deforestation through logging, can have numerous negative health consequences for primates, including increased physiological stress levels (Rangel-Negrín et al., 2014) or reductions in gut micro-biota diversity (Barelli et al., 2015). Devastating tropical storms like Hurricane Maria are expected to increase in both frequency and intensity (Balaguru et al., 2016; Sobel et al., 2016), as well as become increasingly difficult to predict (Emanuel, 2017). Going into the future, studies of how animals adjust, socially or otherwise, to these critical transformations of their environment will be important for addressing the question as to why some species persist while others flounder. The rhesus monkey, which shows impressive proliferation in human transformed landscapes (Richard et al., 1989), will become a critical model in addressing this question.

## CHAPTER 5

### CONCLUSIONS

#### SUMMARY OF FINDINGS

Network dynamics can reveal information about the adaptive function of social behavior and the extent to which social relationships can flexibly respond to extrinsic pressures. In this dissertation, I set out to examine the ways that rhesus monkey (*M. mulatta*) social networks facultatively transform to accommodate various forms of instability. I examined a long-term behavioral data set from the rhesus monkeys of Cayo Santiago island, constituted of nearly 700 unique individuals across six social groups, observed anywhere from 1 to 8 years in length. To this, I applied the tool-kit of social network analysis to characterize individual position within prevailing agonistic and affiliative social networks.

In **Chapter 2**, I set out to evaluate the impact of rank instability as it appears in the day-to-day life of these animals; that is, without any obvious catalyst (e.g., an immigrant male takeover) for instability. I employed a recently developed, network-based permutation method that can establish both dominance rank and, based on the degree of reciprocity that exists within an individual's direct and indirect agonistic encounters, the stability of that rank. I hypothesized that both subordination and the threat of subordination are independently stressful for rhesus monkeys. I found support for this hypothesis, as animals who were low in the hierarchy and

were rank unstable show increased displays of the indices of psychosocial stress (self-directed behaviors, vigilance, and alopecia). This relationship is particularly heightened among males. Furthermore, I examined whether rank instability was an individual property that was recognizable by conspecifics. I found that, independent from dominance rank, monkeys who were rank unstable provoked greater incidence of self-directed behaviors and vigilance when they approached others, suggesting that rhesus macaques are aware of, and made nervous by, this particular brand of uncertainty.

In **Chapter 3**, I examined a highly conspicuous and rare form of rank instability. In early 2012, an unanticipated outbreak of aggression occurred in the Group F female dominance hierarchy and was followed by the eviction of the alpha-family of females—22% of all adult females—into multiple daughter groups. Many of these evicted females succumbed to mortality quickly in exile. I tested the hypothesis that, rather than materializing without clear impetus, this overthrow was actually preceded by deeply seated transformations in social interactions. Interestingly, when I applied the measure of rank instability I had validated in the previous chapter, I found no significant increase in instability in the years leading up to the event. The event itself, however, was characterized by a precipitous drop in stability, which gradually returned to pre-overthrow levels over the following years. I found an increase in the rate of self-directed behaviors as the overthrow approached, indicating greater group-wide levels of anxiety. I also found that females engaged in the same amount of aggression and grooming in the two years leading up to the eviction but that there were clear changes in their choice of social partners. Evicted females became more discriminating in their grooming relationships in the year nearer the split, showing a greater preference for one another and becoming more cliquish. Put simply, the females who would later be evicted continued to range with the rest of

the group as the overthrow approached but were less likely to interact with other group members in an affiliative manner. These results suggest a critical importance of close-kin in weathering rising levels of social instability. These findings have potential implications for understanding group cohesion and the balance between cooperation and competition that mediates social groups.

In **Chapter 4**, I examined how social networks transform in the wake of environmental disaster. In late 2017, Hurricane Maria made landfall onto Cayo Santiago island, causing near-complete deforestation and island fragmentation. I tested the hypothesis that monkeys increase their investments in social bonds as a means of mitigating the stress associated with this drastically transformed landscape. Similar to the analysis of the matrilineal overthrow in Chapter 3, I addressed both changes in the frequency of interactions as well as changes in partner choice. I found that after the hurricane, monkeys spent considerably more time in proximity with one another, and that this probability of proximity continued to increase over the ensuing months. I, however, found inconclusive evidence that, while in this close proximity, individuals invested more into social bonds through allogrooming. I developed a subsampling procedure to generate permuted proximity networks before and after the hurricane, and to these networks I applied a joint-count procedure to assess the degree to which proximity interactions occur between and within certain categories of individuals. I observed that, concomitant with increased proximity rates, proximity networks had more unique pairings of individuals, a more egalitarian distribution of pairings, and, among females, an increased tolerance for genetically unrelated partners. In other words, individuals who were previously isolated in proximity networks became more integrated during the post-hurricane period. Finally, I tested the hypothesis that, as social bonds are an investment, inter-individual variability in the change in sociality rates

would be predicated on social security prior to the hurricane. I found significant support for this hypothesis, with the largest increases in proximity rate being displayed by individuals who were of high rank, rank secure, and received more grooming.

Although this evidence is partially consistent with my initial hypothesis that monkeys become more prosocial to mitigate environmental stress, in Chapter 4 I also presented an alternative explanation that this pattern in sociality was being driven by changes in the availability of leaf coverage. Without this coverage, monkeys were drawn into close proximity to one another to better recover the utility of what remains of this resource. This situation would explain the population-wide increase in proximity rate and stagnancy of the grooming rate. It, however, does not explain why increases in the proximity rate were attenuated in the immediate aftermath of the hurricane, when, presumably, leaf coverage would be at its nadir. It is possible that there might be discrete stages of disaster, where the immediate aftermath of the hurricane exerts special influence. Unfortunately, the present data set is unable to interrogate this idea. In any case, the results strongly support the malleability of social relationships in light of environmental changes, whether they are actively investing in social bonds as a means of mitigating stress, or simply renegotiating their tolerance for others in light of a drastically reduced resource.

## **THE UTILITY OF CASE STUDIES**

In this dissertation, I examined two events of exceptional rarity among rhesus macaques, one social (a matrilineal overthrow) and one environmental (a natural disaster), with the presumption that they would provoke social relations to adapt in similar ways. Evidently this is not the case. Recall in my introduction I had discussed two means in which primates may potentially alter their social bonds in response to changing externalities: they can universally

reduce their social interactions (that is, their frequency) or they can alter their choice of partners (Dunbar, 1991, 1992). In the context of the matrilineal overthrow, females made no changes to their overall rates of interactions, but did refocus grooming efforts on close kin. This is a sensible response considering that the source of instability was emanating from their conspecifics. Alternatively, in the wake of environmental collapse, females showed an increased tolerance (although it is important to reiterate that it still amounted to an active avoidance) of genetically unrelated individuals. At a minimum, this speaks to the vital importance of accumulating case studies such as these, as the observed group wide changes observed might resist generalizability. Group-wide patterns can be shaped by a number of factors, not least of which are idiosyncratic, personality differences between individuals, which can do much to shape the social style of a group (Sapolsky and Share, 2004).

Though rare and difficult to anticipate in prospective research design, researchers are nevertheless behooved to pursue the study of these destabilizing events, as failure to do so can impart critical blind spots in our knowledge of complex sociality. Take for example the matrilineal overthrow that had occurred in early 2012: despite having observers present the previous two years, it arrived largely unanticipated. It was ostensibly catalyzed by the death of the alpha-male, which, combined with the maturation of young females, created a perfect storm of instability. There is no dearth of research that examines the relationship between dominance rank and reproductive success (Majolo et al., 2012), with benefits mostly (and intuitively) going to high ranking individuals. In the case of the matrilineal overthrow, the highest-ranking females were evicted, and nearly half of them subsequently perished in exile. Permanent evictions are important determinants of gene flow and population structure, and can abolish gains in genetic representation during enduring periods of stability.

## ISSUES IN SOCIAL NETWORK ANALYSIS

Figuring prominently in this dissertation is the use of social network analysis (SNA) to characterize social phenotypes within a group. Although some network theoretic approaches make appearances in earlier primate research (Chepko-Sade and Sade, 1979a; Brent et al., 2011), it is not until the past decade that we see the widespread adoption of these methods (Webber and Vander Wal, 2019). SNA is currently poised for even greater usage in the discipline with the development of more automated means of recording interaction data (*e.g.* biologging; Croft et al., 2016) and more complex forms of modeling (*e.g.*, multiplex models: Smith-Aguilar et al., 2018; Finn et al., 2019; longitudinal networks: Farine, 2018). However, their increased usage has not necessarily been met with the proper development of convention in the discipline regarding best-practices. As a result, SNA has inherited many of the familiar issues of statistical reasoning (James et al., 2009) characteristic of null-hypothesis significance testing, one of which I wish to highlight here.

The example that I will use is that of *betweenness centrality*, a node metric that does not make an appearance within this Dissertation but is frequently deployed in primate research. A node's *betweenness* is the proportion of network paths that must pass-through it to connect each node to every other node (Wey et al., 2008; Krause et al., 2009). *Betweenness* is essentially the reverse of the *clustering coefficient* that appears in Chapter 3: individuals with high *betweenness* have partners that are not connected themselves. Traditionally, this measure has been used to describe group "brokers" who connect disparate subgroupings, contributing to total group cohesion (Lusseau and Newman, 2004; Gilby et al., 2013). In other words, individuals with high *betweenness* are deemed "important." However, this is not its likely significance in rhesus macaques. In rhesus, relationships are tightly structured by genetic relatedness, with females directing most of their attention to close kin. Females that find themselves without close-kin,



say through inability of their mother to produce siblings, or just normal mortality, often weakly invest into a diverse sample of unrelated individuals. This frequently grants them high *betweenness* scores, but I would be remiss to say that that female, with so little social capital, is important to a group; just the opposite.

Baked into many of these network methodologies and metrics for describing social positioning are assumptions regarding their biological significance, and researchers must take care to ensure that they are making the right assumptions. To obviate this issue, researchers are behooved to take explicit stances about the significance of the network measures they employ in their research, and how they apply directly to their (also well enumerated) research questions. In doing so, researchers will engender greater transparency, greater convention, and greater assurance that the right tool will find its way to the right job.

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