BIOBEHAVIORAL ORGANIZATION OF INDIVIDUAL ROLES WITHIN
ESTABLISHED GROUPS OF RHESUS MACAQUES (MACACA MULATTA):
IMPLICATIONS OF GROUP STABILITY AND CAUTIONS FOR REMOVAL OF
INDIVIDUALS

by

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Biobehavioral Organization of Individual Roles within Established Groups of Rhesus Macaques (Macaca mulatta): Implications of Group Stability and Cautions for Removal of Individuals

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Arts at George Mason University

by

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DEDICATION

I am grateful to the monkeys at the California National Primate Research Center, not only for their significant contribution to this work but for their sacrifice to better humankind.

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"If I have seen further it is only by standing on the shoulders of giants" - Sir Isaac Newton

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LIST OF ABBREVIATIONS

Association of Zoos and Aquariums .... AZA
Biobehavioral Assessment .... BBA
California National Primate Research Center .... CNPRC
Conservation Breeding Specialist Group .... CBSG
Species Survival Plan ® .... SSP
Taxon Advisory Group .... TAG
International Species Identification System .... ISIS
International Union for the Conservation of Nature .... IUCN

ABSTRACT

BIOBEHAVIORAL ORGANIZATION OF INDIVIDUAL ROLES WITHIN
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INDIVIDUALS

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George Mason University, 2012

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In zoos, recommendations for transferring animals between institutions are made based
on the capacity of individual institutions, the current genetic distribution of the *ex situ*
population of the species, and the long-term sustainability of the population. These types
of human-induced dispersal have the potential to destabilize not only the social group
receiving a novel individual, but the social group from which the transferred individual
was removed and are often, therefore, contrary to the conservation aims of population
management in zoos. Removal of individuals that manage group conflict has been shown
to be deleterious to group stability and cohesion; however, identifying such individuals
has been difficult. Third-party intervention has been described as an important
mechanism for maintaining group stability in group living primates. An individual's
personality, rank, and power style have been shown to be predictors of successful

intervention. This assessment provides analytical results for the distribution and importance of individual roles, particularly dissipaters of social conflict, within rhesus macaque social networks. In this assessment, 36 individuals from 6 different half-acre field cages were identified from a social network dataset based on the count of third-part interventions in non-kin conflicts. For each cage, the top three dissipaters and top three individuals with no dissipation were selected for biobehavioral assessment. The BioBehavioral Assessment program is designed to characterize temperament, emotionality, and behavioral and physiological responsiveness to novel environments and data have been used in multiple studies to understand the causes and consequences of variation in individual temperament and behavioral responsiveness. This assessment identifies individual factors leading to conflict dissipation: temperament determined within-troop and in a novel environment, behavioral and physiological responses to stress, and individual and group-level network measures. This study also demonstrated that conflict dissipaters differed from other interveners because they were posed to behaviorally and physiologically cope better with the stress of unpredictability; that specific social roles were based on individual attributes which influence how the troop agreed on the dominance status of that individual, which also contributed to a successful intervention; and suggested that males engaging in conflict appeared to play a role in dissipation, whereas female engagement in non-kin conflict was seemingly more complex and requires continued investigation

I.   LITERATURE REVIEW

Many wildlife populations in their natural habitats are declining daily and therefore modern, accredited zoos – those zoological institutions meeting the standards of the Association of Zoos and Aquariums and which seek to play an important role in conservation through cooperative breeding, public education, and scientific investigation – are becoming the beacon of conservation. Modern zoos do this through engaging local communities, maintaining *ex situ* biodiversity, and providing resources and capacity to *in situ* conservation efforts [Baker 2007; Conway 2007]. However, these objectives are not achieved unless zoo populations are maintained in optimum health – physically, genetically, and behaviorally. Zoos and marine parks routinely assess multiple aspects of species' characteristics for the purposes of population, genetic, and collection management and to meet conservation aims [Ballou et al. 2010; Soule' et al. 1986]. For many social species commonly housed in groups, such as primates, ungulates, marine mammals, and avifauna, there is often a compromise between the sustainability of the *ex situ* population and the well-being of individual groups at multiple institutions [Ballou et al. 2010].

Transferring animals between institutions has effects on both sides of the transaction, particularly with social groups. Such disturbance to social groups occurs through fragmentation of the departing social group and introduction of a novel individual into the acquiring social group. Group fragmentation and instability has the potential to distract from normal reproductive behavior, therefore likely reducing reproductive output, which is contrary to the initial conservation aim. A more comprehensive understanding of the social roles individuals play within social groups could be useful to population managers by adding another level of analysis between population and meta-group viability. Individual differences in behavioral types (i.e., personality, temperament) may not only cause variation in social structure, but be an important component of social stability.

For social species of concern, small disruptions to group stability could be detrimental to the sustainability of that group and further the population as a whole – a valid concern when accounting for required manipulations of social groups to better understand the effects of population management practices. The matrix between behavioral traits and network characteristics can deduce many informative patterns important to population management, such as the position of personality traits in the consistency of network position, links between personality and position in social cohesion, and the effects of role removal in concerns to social aggression and group stability. Understanding the distribution of individual roles within a group could be an

accurate measure of group stability by showing the relationship between behavioral type and manifest aggression and affiliation within a social network.

1.1   Population Management in Zoos

Zoos acquire animals three ways: (1) from birth, (2) by purchase or loan from a third party, or (3) from the wild. In the past, collection from the wild was not uncommon; however as wild stocks decreased, zoos have sought alternative resources for increasing, diversifying, or maintaining their animal collections. Today, zoos focus on increasing their populations through participation in cooperative zoological breeding programs or form other managed breeding facilities and as a result, most animals in zoos today are captive born [Ballou and Foose 1996; Ballou et al. 2010; Foose 1980]. The focus of zoos, therefore, has moved from exhibiting a high diversity of species to public education and breeding programs for the conservation and management of species.

As zoos modernize their infrastructure, multiple older exhibits are replaced with larger enclosures that better meet the needs of the species it houses, which often reduces the zoo's carrying capacity [Baker 2007]. Collection planning is an important component of the functioning of a zoo. The variety of species a zoo cares for depends on the nature of the zoo. Capacity, public opinion, and visitor attraction also drive zoo collection planning [Baker 2007; Balmford 1996; Conway 1986]. Because each zoo has different

needs in regards to these three criteria, zoos as a collective strive to maintain sustainable populations through managing metapopulations (sets of local populations connected by dispersing individuals [Hanski and Gilpin 1991]). Smaller populations experience higher probability of extinction; however, extinction becomes less likely if the discrete groups are managed as a collective through individual migration. From this standpoint, the interests of the species being conserved may supersede the interest of an individual institution and the individual animal.

1.1.1   Why Manage Ex Situ Populations?

Managers need sound rationale and criteria for guiding the management of species maintained in zoos. Media, watchdogs agencies, and government regulators shape public perception [BoardSource 2005]; therefore, as most zoos are accountable to public standards, these operators influence the evolution of zoo management practices. Recommendations for the transfer of individual animals among institutions are based on the long-term conservation goals of maintaining genetic diversity and demographic security [Ballou and Foose 1996; Ebenhard 1995; Weise et al. 1996]. The promotion of genetic diversity through population and demographic management ensures a population is able to adapt to changing environments [Ballou and Foose 1996; Hendrick et al. 1986; Vrijenhoek and Leberg 1991] and are free of the deleterious effects of inbreeding [Lande 1993] and low levels of genetic variation [O'Brien et al. 1985; Wildt et al. 1987].

The focus of metapopulation management is to reduce the rate of loss of genetic diversity and heterozygosity [Ballou and Foose 1996; Ballou et al. 2010; Foose 1980; Lees and Wilcken 2009; Margan et al. 1998]. The genetic diversity within a population is the allelic-composition of the established population, and is often compared to the expected composition of the founding wild population [Ballou et al. 2010; Lande 1988; Shaffer 1981; Soule' et al. 1986]. Individuals are selected to be bred based on specific measures of genetic diversity known as mean kinship [Ballou and Foose 1996; Ballou et al. 2010; Earnhardt et al. 2001; Margan et al. 1998; Montgomery et al. 1997]. Loss of heterozygosity is related to an individual's inbreeding coefficient, or how related an individual is to others within the population. Therefore mating the least related individuals in a population reduces the rate at which heterozygosity is lost [Baker 2007; Ballou and Foose 1996; Montgomery et al. 1997; Soule' et al. 1986]. The standard format for selecting mate pairs is first prioritizing animals with low mean kinship and then rejecting the pairs whose offspring would have high inbreeding coefficients [Soule' et al. 1986]. From this standpoint the guiding principle in population management is that the higher the level of genetic diversity in a population the lower the critical level for inbreeding – both of which are a function of time. Soule' et al. [1986] suggested a strategy of maintaining 90% of founding genetic diversity over a period of 200 years to ensure *ex situ* populations will be fit for repatriation when human population growth has stabilized. Due to the small size of populations in zoos, this formative strategy has been refined to 90% diversity for 100 years to accurately represent achievable population and demographic management goals [AZA 2011a; Ballou et al. 2010].

Inbreeding in *in situ* populations is reduced by dispersal of individuals from their native group before reaching sexual maturity [Pusey and Wolf 1996]. The absence of dispersal increases the abundance of non-natal mate choices and has implications on the physical health of a group and the genetic health of the population [Ralls et al. 1988]. For example, the physical health of a group can be compromised through the mechanism of inbreeding depression in which deleterious recessive genes can be unmasked [Ballou et al. 2010; Ralls et al. 1988]. Inbreeding is a primary welfare concern as its effects may include reduced longevity, physical malformation, metabolic and immune diseases, modified temperament, and increased susceptibility to stress [Ballou et al. 2010; Fagen and Holmes 2006; Foose 1980; Lande 1988; Lande 1995; Margan et al. 1998; Montgomery et al. 1997]. The genetic health of the population may suffer from the lack of genetic diversity in which to maintain long-term evolutionary potential of the species, which influences how well a population can rebound from stochastic (random) environments or catastrophe [Ballou and Foose 1996; Ballou et al. 2010; Lande 1988; Lande 1993; Lande 1995; Shaffer 1981].

Some zoos have addressed the health and genetic risks of managing closed populations by implementing cooperative breeding programs [AZA 2011a; Lees and Wilcken 2009; Margan et al. 1998; Seal et al. 1994; Soule' et al. 1986; WAZA 2005]. These cooperative population management programs address concerns regarding the trend of resource relocation from coordinated population management to *in situ* conservation efforts over the last decade [Baker 2007; Lees and Wilcken 2009]. They

also address the prevalent low levels of genetic diversity and population sizes [Baker 2007; Ballou et al. 2010; Hutchins et al. 2002; Magin et al. 1994]. Resource relocation and low levels of genetic diversity bring some to question the efficacy of past zoological population management efforts. Regardless, the science of meta-population analysis is sound and has been employed successfully with many managed species [Foose 1980; Lande 1995; Magin et al. 1994; Margan et al. 1998; Montgomery et al. 1997] and zoos worldwide are enacting plans to mitigate these concerns by continued action and refinement of population management practices [see AZA 2011a; WAZA 2005].

1.1.2   Population Management within the Association of Zoos and Aquariums

Association of Zoos and Aquariums (AZA) accredited facilities manage populations through a hierarchical series of programs based on species studbooks (routinely updated registrar of species pedigree, demographic history, and all information relevant to the managed population), including Taxon Advisory Groups (TAG) and Species Survival Plan® (SSP) Programs. These programs assist in coordinating various aspects of a species husbandry, veterinary, and behavioral needs as well as establishing cross-institutional metapopulation, demographic, and genetic viability and sustainability goals [Allard et al. 2010; AZA 2011a; Ballou et al. 2010; Lees and Wilcken 2009].

Taxon Advisory Groups: In North America, TAGs evaluate the needs of taxa in zoos and aquariums and provide facilities with population management and conservation recommendations based on the genetic and demographic health, and therefore the long-term viability, of the population. TAGs develop Regional Collection Plans (RCPs) which recommend species for *ex situ* management amongst AZA institutions [Allard et al. 2010; AZA 2011b].

Species Survival Plan® Programs: SSP Programs manage and conserve select species in *ex situ* populations at differing levels. Species are internally designated as green and yellow levels based on the ability to maintain 90% genetic diversity for the next century and a set minimum number of individuals. The more than 300 SSPs develop Breeding and Transfer Plans that set population management goals and recommendations to participating AZA institutions [AZA 2011a].

These programs work in conjunction with international-level programs such as the World Association of Zoos and Aquariums (WAZA), the International Species Identification System (ISIS), and the Conservation Breeding Specialist Group (CBSG). For example, WAZA maintains a program of international studbooks which monitor populations and guide management practices for 123 active international studbooks. The ISIS Central Database constitutes institutional holdings from nearly 825 institutions in over 76 countries which routinely submit electronic specimen reports. Additionally, the development and implementation of new ISIS software for collection management and

monitoring, called Zoological Information Management System (ZIMS) will further

integration and data sharing amongst the international community and advance

knowledge of individual animal history to inform breeding recommendations, among

other advantages. The CBSG was organized by the Species Survival Commission (IUCN)

to advise, monitor, and catalyze international propagation [IUCN/CBSG 1993]. Using

collected information, including the ISIS Central Database, the CBSG fosters, integrates,

and coordinates *in situ* and *ex situ* conservation efforts. Though WAZA, ISIS, and CBSG

(among others) maintain roles separate from AZA, these organizations provide a world-

wide cooperative infrastructure to species population management. For example, national

and international cooperative population management can be used to inform quantitative

analysis of genetic and demographic data to develop informed management plans carried

out through recommendations for each species world-wide.

1.1.3   Considerations for Social Group Management

There is more to maintaining populations than making breeding recommendations

based on genetics and demography [Carlstead and Shepherdson 2005; Hediger 1982;

Kleinman 1994b], as behavior plays an important role in propagation and reproductive

behavior [Allard et al. 2010; Carlstead and Shepherdson 2005; Kleinman 1994b;

Shepherdson 1994]. However, no practical measure of group or individual behavior

exists to assist population managers in refining decision making for the population.

Inherent to the conservation aim of maintaining *ex situ* populations is the preservation of

natural behavior – a factor that should be considered in making breeding selections [Hediger 1982], even more so for social species. Inappropriate social environment, such as disproportionate sex/age ratio, has important implications to the reproductive success of *ex situ* social species [Kleinman 1994a; Lyndburg and Fitch-Snyder 1994; Moberg 2000; Stobbkof 1983]. Further, the mating systems in mammals specifically are diverse [Birkhead and Parker 1997; Clutton-Brock 1989; Wilson 2000], and few mammals have been classified as monogamous [Clutton-Brock 1989; Wielebnowski 1998]. Therefore, selection of individuals for reproductive pairing based solely on genetic and demographic considerations may conflict with mating strategies and be unproductive [Grahn et al. 1998; Wielebnowski 1998].

Maintaining appropriate social contingencies are particularly important for nonhuman primates as all primates reside in some form of social group [Muller and Soligo 2005; Muller and Thalmann 2000; Pimley et al. 2005]. Although the environmental pressures that predicate the formation of social groups in the wild (e.g. habitat type [Crook and Gartlan 1966; Hill and Lee 1998; Richard 1985], activity cycle [Muller and Soligo 2005; Richard 1985], predation [Muller and Soligo 2005; Wilson 2000], and access to food and social partners [Isbell and Young 2002; van Schaik 1983; Wrangham 1980]) are not present in most *ex situ* primate populations, other challenges are present. These include limited space, decreased ability to make social adjustments to alleviate social tension, and decreased ability to find suitable breeding partners [Price and Stoinski 2007].

Even with an appropriately sized social group, the reproductive and psychological needs of an individual may not be met if the structure and composition of the group are inappropriate [Price and Stoinski 2007]. For example, in some nonhuman primates, suppression of reproduction has been contributed to familiarity with other group members and the age of introduced members [Epple 1970; Robbins 1996; Stoinski et al. 2004a; Stoinski et al. 2004b]. Further, some natural social systems, such as polygynous (one male with primary access to multiple females) species or fission-fusion (multiple groups that routinely cluster and separate) systems, may result in additional difficulties in *ex situ* populations, which include the management of surplus males [Price and Stoinski 2007; Stoinski et al. 2004a; Stoinski et al. 2004b] or high rates of intergroup aggression [Alford et al. 1995; Bloomsmith and Baker 2001; de Waal 1989; French and Inglett 1989; Inglett et al. 1989]. Lastly, the arrangement of social groups and novel animal introduction requires flexibility and knowledge of natural primate migratory and dispersal patterns and the ability to replicate similar movements with population management methodologies [Alford et al. 1995; Price and Stoinski 2007; Stoinski et al. 2004a; Stoinski et al. 2004b].

Individuals likely play important roles in the composition, and therefore appropriateness, of social grouping. The basic structure of social groupings relies on the behaviors needed to attain and maintain dominance (e.g., affiliation versus agonism), the intensity and frequency with which such behaviors are expressed, and the alternatives available to dominance. Contrary to popular thinking, the most aggressive individuals

within a primate social group are generally not the most dominant, but instead are those individuals attempting to find a place within the hierarchy [Altmann et al. 1995; Richard 1985; Wilson 2000]. The mechanisms underlying what is involved in being dominant or subordinate in a particular primate society may be best ascertained through the dichotomy between stable and instable social groups or hierarchies [Chamove and Bowman 1976].

The mechanisms of stability in nonhuman primates are still uncertain [Beisner et al. 2011a] however degree of conflict resolution or reconciliation [de Waal 2000], interference by third parties [Flack et al. 2005; Flack et al. 2006b], and group size and composition [Dazey et al. 1977] likely play key roles in maintaining social cohesion. Kinship has been shown to lend an organizational relationship to nonhuman primate dominance [Beisner et al. 2011a; Cheney 1977; Horrockes and Hunte 1983; Kanngiesser et al. 2011; Missakian 1972] and affiliation [Beisner et al. 2011a; Gouzoules 1984; Kanngiesser et al. 2011] relationships. If kin-based social structures are augmented by the removal of individuals for the purposes of population management, social instability may be a result. Instability is seen when dominance shifts between individuals or kin groups and has been demonstrated by high rates of inter-group aggression and the fissioning of the group [Beisner et al. 2011a; Flack et al. 2006b; Inglett et al. 1989].

Aside from the importance of dominance relationships, a burgeoning aspect of social stability is the influence of different personality styles on group cohesion [McCowan et al. 2011]. For example, individuals showing consistent affinity towards

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forming affiliative relationships, showing a high degree of social intelligence, or exhibiting markedly reduced impulsivity control will influence the stability of the social group of which they reside. New tools for managing social groups, such as social network analysis [McCowan et al. 2008; Oates-O'Brien et al. 2010], are being developed, which intend to bridge the gaps between managing populations, groups, and individuals.

1.2   Studies of Social Network Analysis

Social network analysis allows one to visualize the patterns of relationships among members of a group, community, or system and quantify the nature of these patterns as well as the roles of individuals [Wasserman and Faust 2005]. Social networks may be constructed for many different types of relationships or actions of consequence, such as mutualistic, agonistic, cooperative, sexual, and other interactions. These relationships are represented graphically by drawing lines (aka edges) between two individuals (aka nodes) that have a particular relationship. [Croft et al. 2008; Wasserman and Faust 2005]. Edges can represent simple presence or absence of a relationship, or they can include information on intensity, frequency, direction, and relative distribution of interactions across social levels of organization (i.e. population, group, or individual). A set of edges can therefore discern manifest patterns of relationships within a network. Network measures can then be calculated based on the values of edges which allow comparative, quantitative (statistical), or qualitative (graphical) hypothesis testing [Krause et al. 2007; Scott 2000; Wasserman and Faust 2005] on otherwise structurally

complex relationships [Croft et al. 2008]. The social network approach thus allows us to investigate indirect, individual-level interactions as well as effects on social structures at the population-level [Croft et al. 2008].

There are a number of network measures that can provide information about the stability of a group and the role of an individual within the group, such as clustering coefficients, degree centrality, and betweenness centrality. Clustering coefficients can be calculated and act as an average measure of local-group structure. Clustering coefficients occur at two levels: node and network. The clustering coefficient for each node is the number of connections (i.e. triangles) of which the node is apart. Similarly, the network clustering coefficient is the average of the node clustering coefficients, and therefore a measure of local "cliquishness" [Croft et al. 2008]. Well-connected nodes tend to maintain positions central to the network, indicating individuals that are the most important or central to the network. These positions are said to hold the network together [Croft et al. 2008; Scott 2000; Wasserman and Faust 2005]. Node betweeness is another measure of centrality which calculates the number of shortest paths passing through the node. Because betweeness does not simply measure paths connecting nodes on either side of the node it is a sensitive discriminator of the relative position of the node and further assists in identifying key nodes within the network [Croft et al. 2008; Scott 2000; Wasserman and Faust 2005].

Central nodes are not the only important role within a network. Croft et al. [2008] described entities that connect two separate groups as 'cutpoints'- individuals that not only hold a position that unifies a network, but also facilitate exchange between otherwise disconnected groups. In social network analysis, cutpoint entities are at the extremes of betweeness centrality in that these individuals are involved in the majority of paths between different members in the network. Therefore, key social roles are identified by the inequality of prominence (centrality, betweeness) across a network [de Waal 2002; Lusseau and Newman 2004]. The reach of a social role, defined as the number of nodes two or fewer steps away (indirect connectedness), is also important in determining the importance of a social role because it describes the influence (through number of edges) a role has on aspects of the network [de Waal 2002; Flack et al. 2006a].

This framework allows for an improvement over traditional dyadic interactions, refining management methodologies to include aspects of indirect relationships – i.e. intermediate relationships [Krause et al. 2010; McCowan et al. 2008]. Wilson [1975] was the first to see value in social network approaches in animals, however the application of social network methodologies did not gain prevalence until the 1990's [Sade and Dow 1994; Scott 2000; Wasserman and Faust 2005]. Several recent reviews demonstrate the efficacy of social network analysis in multiple fields of animal behavior, socioecology, health, and primatology [Brent et al. 2011; Krause et al. 2007; McCowan et al. 2008; Sih et al. 2009; Sueur et al. 2011; Wey et al. 2008].

1.2.1 *Social Roles and Group Stability*

Group stability may not necessarily rely on the most dominant animals, those that are generally central to network and whose role in the network is agreed upon by other highly connected individuals. Other influential factors of less dominant group members, attributable to the individual level, are likely at play such as their participation in initiating or dissipating conflict, personality, and gender-specific dominance characteristics. Due to their prominence and facilitative characteristics, each of these individual factors can be identified as a key social role and can affect network cohesion. Nevertheless, the interactions between these key social roles and network cohesion and stability in nonhuman primate networks are just now being understood.

For example, Flack et al. [2006a] has shown the importance of impartial policing (third-party intervention into conflicts without favoritism) as an important mechanism of stability in nonhuman primate social networks. Individuals with high social power, as indicated by the receipt of higher than normal number of unidirectional subordination signals (i.e., silent bared-teeth display) and a high degree and reach (i.e., many partners), directly controlled the transmission of aggression throughout the social network. Interestingly, when conflict 'policers' are temporarily removed, groups within the network constrict (i.e., increase clustering, show lower degree of social integration), and inter-group rates of aggression increase. Thus, network fragmentation can be defined as the inverse of connection redundancy within a network [Borgatti 2003]. Flack et al.

[2006a] suggest the lack of policing leads to high conflict frequency and more conservative social interactions. Likewise, individuals that connect to other well-connected individuals act as a center point of the network and, likewise, are important in maintaining network cohesion through intervening on agonistic interactions.

The Flack et al. [2006a] study showed only high-ranking males tend to be successful interveners, however other factors besides sex likely contribute to intervention success. For example, the high agreement of the individual's dominance amongst the social network (as measured by social power) and the larger size of male macaque monkeys combined likely contribute to the low risk of retaliation from intervention. However, high-ranking males are not the only successful interveners in macaque social networks suggesting factors in addition to rank and sex are present. McCowan et al. [2011] investigated (1) which individuals attain high social power and (2) of those that attain social power, which individuals become successful interveners. The study supported third-party intervention as a mechanism of social stability and demonstrated that individuals higher in social power are more successful when intervening in conflict. Additionally, the study showed an individual's personality and their likelihood of intervention success were also highly correlated. However, this correlation differed between males and females. Equable males with high social power were more likely to successfully intervene in conflict than bold or excitable males. Females, on the other hand, showed no differences in intervention success and social power across personality types and showed much less success in intervention than males overall.

The discrepancy between successful interventions, personality, and sex can be attributed to how each gender attains dominance in rhesus macaques [McCowan et al. 2011]. Free-ranging rhesus macaque populations are characterized by female philopatry (remaining with natal groups) and male dispersal [Drickamer and Vessey 1973; Fooden 2000]. Females form dominance hierarchies according to their matrilineal kinship. Dominance is passed through these matrilines from mother to daughter and generally remains stable throughout a lifetime. Males dominance, on the other hand, is based on age, body size, and group tenure and is therefore unstable over a lifetime [Boelkins and Wilson 1972; Drickamer and Vessey 1973; Sprague 1992; Sprague 1998]. Regardless, aggression is used by both sexes to establish and reinforce dominance relationships [Fa and Lindburg 1996; Thierry et al. 2004].

In *ex situ* environments, the differences between sexes in the attainment of rank and the role of males in decreasing intergroup conflict and aggression is hampered by the inability to naturally disburse. In free-ranging macaque populations, males can either enter a group and work their way up a hierarchy [Drickamer and Vessey 1973; Vesey and Meilke 1987] or challenge the resident dominant males for rank [Lindburg 1969; Neville 1968]. Natal males, those inhibited from naturally dispersing, have been shown to utilize alternative strategies such as forming maternal kin alliances to challenge older, larger males, to quickly rise in rank [Beisner et al. 2010; Koford 1963]. Further, younger natal males from more dominant matrilines in particular have been shown to initiate more frequent and intense aggression [Beisner et al. 2010].

The ability to identify individuals that maintain group stability is relevant to management decisions. From a population management perspective, identifying key social roles that maintain group stability is important because removing social components identified as central to the network could have important consequences on the stability of the network [Beisner et al. 2011b; Croft et al. 2008; Flack et al. 2006a; Lusseau and Newman 2004; McCowan et al. 2011; Wasserman and Faust 2005]. As shown by McCowan and colleagues [2011], personality likely has an important function, though the relationship between personality and network positions is relatively unknown [Krause et al. 2010].

1.2.2   Social Networks for Managed Systems

The focus on indirect patterns and relationships is what makes social network analysis an intriguing tool for managing animal populations. The ability to analyze indirect or complex patterns furthers the advantages of social network analysis in population management. For example, because rhesus monkey females are known to be the worst instigators of deleterious social aggression, McCowan et al. [2008] expected groups with higher proportions of adult females to show lower social power or higher network fragmentation. They showed that a more even distribution in the number of individuals within a matriline (i.e. less despotic social structure) exhibited higher consensus over dominance relationships and promoted social cohesion. These results were seen in both grooming and conflict networks, suggesting that the appearance of

network fragmentation, reduced social power, and decreased grooming reciprocity may be indicators of social instability and may be measures used to longitudinally monitor social group dynamics and predict deleterious aggression.

Individual attributes can add an important dynamic to the assessment of social networks in animal management [McCowan et al. 2008]. As discussed above individual properties (i.e. personality) can provide a quantitative measure to network statistics. For example, the tendency of individuals with similar behavioral types to connect to one another [Croft et al. 2008; Krause et al. 2010; McCowan et al. 2011; Newman 2003] or the manner in which characteristics of personality are distributed throughout a community's structure [Krause et al. 2010; Wolf et al. 2007] could show how an individual's attributes within one network correlate to similar tendencies within other networks. The reliability of such measures of cross-network generalizations have not been thoroughly investigated, however, and should be viewed cautiously [Croft et al. 2009; Krause et al. 2010]. Additionally, an individual's interaction outcome may not be a product of that individual's own control but a result of other animals behavior towards it [Piyapong et al. 2010]. In such instances dyadic interactions may be the best source of confirmation [Krause et al. 2010]. Lastly, the link between personality type and the context of social cohesion likely have population-level consequences which are mostly unknown.

1.3   Studies of Nonhuman Personality

Managing attributes and differences between individual animals generally occurs informally on a case-by-case basis; however this process can be formalized to enhance genetic diversity, demographic management, and well-being. Watters and Powell [2011] suggest it is possible to develop programming within current population management software that accounts for behavioral typing at species or family levels for the purposes of goal setting and population management [Watters and Powell 2011; Lacy, Ballou, Long, Watters, and Powell, *in preparation*]. This increased focus on personality may give zoos and other *ex situ* environments added support to further investigate the efficacy of personality in animal management and to fill in the current gaps in knowledge.

The diverse, multidisciplinary approaches investigating nonhuman primate personality has given the field as broad a range of methodologies as it has diversity in research literature [Freeman and Gosling 2010]. The distinction between personality and temperament has not maintained consistency in nonhuman primate or animal personality literature, and its potential implications are otherwise too broad and not necessarily relevant for the scope of this review (see Freeman and Gosling 2010; Gosling 2001), therefore the term personality will be used as synonymous with temperament to maintain clarity.

Though there is no consensus on the definition of animal personality, it has been traditionally defined as behavioral response conditions that are constant over time and situation [Capitanio 1999; Gosling and John 1999] where behavioral responses can be

described by within- and between-individual consistency in behavior at the group level [Sih et al. 2004]. In other words, an individual's behavior can show consistent variation from situation to situation, which can be an organizing influence over the individual's behavioral responses. From the standpoint of a population, individuals vary in the degree to which they express a particular personality trait, and therefore traits can be organized in hierarchical taxonomies describing the structure of personality within a population [Uher 2008]. From these definitions, behavior is context specific whereas personality is a set of stable characteristics that motivate an individual's behavioral reactions. This belief stems from the view that behavior is mediated on the individual's needs and desires weighed against the opportunities and constraints of the environment [*sensu* Capitanio 2004].

Investigations into nonhuman primate personalities are not a recent phenomenon. Stevenson-Hinde and Zunz [1978] were the first to assess and rate nonhuman primates using descriptive definitions and a scaled scoring system. Their system has been adapted and modified to rate personality in nonhuman primates including rhesus [Capitanio 1999; Capitanio and Widaman 2005], stump-tail [Figueredo et al. 1995], and pig-tail [Caine et al. 1983] macaques; gorillas [Gold and Maple 1994; Kuhar et al. 2006]; chimpanzees [Dutton 2008; King and Figueredo 1997; Weiss et al. 2009]; vervets [McGuire et al. 1994]; and capuchins [Byrne and Suomi 2002] to name a few. With this, the vast majority of personality studies on nonhuman primates (approximately 40%) have been conducted on rhesus macaques [Freeman and Gosling 2010].

Rating systems (41% of studies [Freeman and Gosling 2010]) are a subjective

approach which utilizes experts on the species who, through their cumulative experience,

assess individuals based on adjective descriptors, generally via a likert scale. For

example, an individual may be rated high in sociability' and low in 'cautiousness.' Raters

are expected to be familiar enough with the subjects so that their impression represents a

reasonable view of the individual's personality. The main limitations of descriptive

ratings of personality are inter-observer agreement and the large sample sizes of surveys

for analysis; however the system captures indirect observations potentially not accounted

for in coding systems. On the other hand, coding systems (comprising between 74%

[Gosling 2001] to 89% of studies [Freeman and Gosling 2010]) involve direct behavioral

observation in a naturalistic or testing situation. Behaviors expressed in different

situations are correlated and are therefore more objective. Coding systems are limited in

both time and breadth, as observations are generally conducted between start and end

dates and in accordance to a pre-determined Ethogram. However the multivariate data

collected are not dependent on observer expertise and can be evaluated in a variety of

manners.

In a comparison of adjective descriptors with behavioral ratings, Uher and

Asendorph [2008] concluded that descriptive ratings account for the most amount of

variation in behavior, and therefore contribute to a larger predictive range of behavior.

Ideally, descriptive ratings accompany how an individual will approach a situation and

describe the likelihood of response under certain conditions irrespective to the

individual's age, sex, reproductive status, and other temporal, environmental, and physiological components driving behavior. Adjective descriptors, from this standpoint, are an individual's underlying approach to responding to the environment, and function to determine the patterns of behavioral traits within a population. Uher [2008] indicated behavioral coding assessments, on the other hand, identify representative trait dimensions that are measurable with multiple methods of direct observation and account for both patterns and positioning of traits within a population. Further, because behavioral measures are easily visible by trained observers they are less likely to be affected by manifest theories of personality. The combination of descriptors and behavioral coding nullifies the ambiguity if this chicken-and-the-egg scenario, though only a few longitudinal studies exist (see Capitanio 1999). As research from the recent boom in personality studies mature, the temporal divide is likely to diminish and research outcomes will become more refined.

1.3.1   Personality Assessments in Zoos

Zoo animal behavior has been examined for decades [see Watters and Powell 2011]. Zoos may enhance the investigation of personality by expanding the environments in which personality can be studied to better understand how well personality traits and dimensions generalize across populations and environmental contexts. Zoos can inform not only the applied aspects of personality assessments (e.g. managing individual and population health and well-being), but add to the biological, developmental, ontogenetic,

and environmental influences on personality. Likely the biggest effect zoos can have on the study of personality is identifying measures for studying interspecies personality traits which are underdeveloped [Capitanio 2004; Uher 2008; Uher and Asendorph 2008].

Currently, two approaches dominate the development of personality rating instruments across species [Freeman and Gosling 2010; Gosling 2001]. The 'emic' approach generates rating instruments for a particular species. The Stevenson-Hinde and Zunz [1978] study is an example of this where the adjective descriptors and behavioral measures were developed from observation of rhesus macaques and the analyses were not directly based on methodologies found in human or other nonhuman studies on personality. Conversely, in the 'etic' approach, instruments that have been developed for one species are applied to assess personality in another. The Stevenson-Hinde and Zunz [1978] study is another good example, with 40% of nonhuman primate [Stevenson-Hinde and Zunz 1978] personality studies citing use or slight modification of this study. The emic and etic approaches both have associated benefits and risks [Gosling 2001; Gosling and John 1999]. The emic approach is more laborious than the etic, however the measures and traits derived are likely more representative of the particular species being studied. The requisite of the etic approach is a comprehensive understanding of the species. For example, if a trait is seen in one species and not another the investigator would be forced to ascertain whether the trait is inherited from a common ancestor or is convergent based on similar ecologies [Gosling 2001].

Any assessment involving cross-species comparisons must account for aspects of behavior, ecology, ontogeny, and other species-specific influences limiting similarities. As previously discussed, the combination of adjective descriptors and behavioral ratings likely account for such variation, and selecting statistical models which accurately explain unique within-species aspects further refines these methods. Cross-species comparisons of personality require measurement of the position of a trait within a trait hierarchy for the species, more so than the patterning effects of the population, therefore descriptive ratings are insufficient alone [Capitanio 2004; Uher 2008].

Secondly, due to the nature of personality and its limited methodological approaches, the reliability of this science will be enhanced through replication on multiple groups of the same species in different environments. The descriptors and rating instruments employed reliably in one species may not be reliable in another. Therefore, these instruments, may suffer in construct validation as they will not measure what is intended to be measured. In the end, etic approaches that have not readily accounted for species-specific differences must be viewed cautiously.

Lastly, adjective descriptors, though they are often composed from behavioral ratings and have shown to be reliable, should be weary of anthropomorphic tendencies. This is particularly true within zoos and aquariums, where personality ratings assigned to individuals as a management tool could be misconstrued through misunderstandings of the adjective descriptors, and thus inhibit effective decision-making. For example, when

assessing personality in large carnivores to inform introduction procedures an individual

with a personality descriptor of sociability was scored as both moderately low anti-

asocial by one evaluator and moderately social by a second and third evaluator [Russell-

White and Minier *in preparation*]. Sociability was misunderstood as level of aggression

towards humans, and a disparity existed between the evaluator's level of experience with

the animal (i.e., the first evaluator was a part-time relief caretaker and the other two had

worked with the animal for several years). Not investigated, implications such as these

would indicate this animal was less of a candidate for social pairing. Therefore,

personality assessments in zoos and aquariums should be employed judiciously.

II. INTRODUCTION

Human-induced dispersal in managed animal populations has the potential to fragment social groups through the removal of individuals playing key social roles. Individuals who successfully intervene on intergroup conflict, who have previously been identified as conflict policers [Flack et al. 2006a; McCowan et al. 2011], play such crucial roles in managing social groups. Additionally, the absence of natural dispersal in these populations can be a cause for concern as genetic relatedness, age and sex characteristics, and natal alliances also contribute to conflict [Beisner et al. 2010; Beisner et al. 2011a; Beisner et al. 2011c; McCowan et al. 2011]. To ensure sustainable *ex situ* populations, more information is needed regarding the mechanisms of social group cohesion at the individual level.

Individual attributes may add an important dynamic to the assessment of social networks for animal management [McCowan et al. 2008]. For example, individual properties, such as personality, may provide quantitative measures to network statistics such as the tendency of individuals with similar behavioral types to connect to one another [Croft et al. 2008; Krause et al. 2010; Newman 2003]. This can also be seen in how personality sorts itself throughout the community structure [Krause et al. 2010; Wolf et al. 2007]. Dominance, as an important aspect of maintaining social structure, is determined by skill in negotiating social stressors such as an individual's ability to predict and control social circumstances. Sapolski and Ray [1990] found that the most dominant male baboons had lower cortisol compared to other dominant males, suggesting

a neutral physiological response to social stress. Lower arousal likely leads to these dominant males' ability to differentiate between neutral and threatening social stimuli, distinguish between winning and losing a fight, or displace aggression to a third party.

When individuals in a social group interact over a period of time, a certain degree of predictability inevitably develops. In other words, future interactions between individuals are more likely to be reflective of past interactions than they are to be completely novel. For example, cumulative wins are known to influence an individual's engagement of future aggressive acts as well as the outcome of subsequent contests in many species [Beisner *unpublished*; Hsu et al. 2006]. However, Sapolsky and Ray's dominant males exhibited similar behavioral and endocrine patterns over a number of years, suggesting multiple styles of dominance were present based on individual attributes [Sapolsky 1983; Sapolsky and Ray 1989, 1992]. Likewise, McCowan and colleagues [2011] showed that personality influences the relationship between social power (a measure of troop agreement on the dominance of an individual as indicated by how often an individual receives unsolicited signals of subordination) and successful intervention of third-party conflict in rhesus macaques. They hypothesized that bold males receive subordination signals because of their frequency of approach to group members where individuals characterized as excitable receive signals because they are unpredictable. Equable males, on the other hand, likely receive signals because they are respected or popular members of the troop and were more successful interveners in conflict than bold or excitable males.

These examples demonstrate that some individuals play an integral role within a social network and this is determined by (1) individual personality, (2) their interconnectedness across the social group, and (3) their interaction dynamics with other individuals within their group [Croft et al. 2008; Newman 2003]. How an individual's attributes within one network correlate to similar tendencies within other networks is relatively unknown [Croft et al. 2009; Krause et al. 2010]; therefore, the effects of consistency in personality and its associated effect on network position need to be viewed cautiously. Additionally, an individual's interaction outcome may not be a product of that individual's own control, but a result of other animal's behavior towards it [Piyapong et al. 2010]. In such instances, dyadic interactions may be the best source of confirmation [Krause et al. 2010]. Lastly, the links between personality type and the context of social cohesion likely have mostly unknown consequences on group and population levels [Krause et al. 2010]. To avoid these pitfalls, this study focused on the correlation between the attributes of an individual rather than focusing on the role an individual holds within the group as a whole.

2.1   Research Objective

This study examines how the interaction of personality traits and social roles in rhesus macaques affects the ability of individuals to dissipate third-party, non-kin conflict. Third-party intervention has been described as an important mechanism for maintaining group stability in group-living primates. To date, much of what is known about how individual characteristics influence successful third-party intervention comes from the assessment of personalities while individuals are interacting in their social

groups. This study departed from this standard type of assessment by assessing individuals in a novel environment to investigate personality in relationship to an individual's reactivity to challenging stimuli. Further, this study specifically investigates interveners to identify reactivity traits that are associated with successful intervention outcomes, i.e. dissipation of conflict. Data were utilized from two ongoing programs of assessment (Biobehavioral Assessment, Social Network Analysis) at the California National Primate Research Center (CNPRC).

2.2   Hypotheses and Predictions

This study assesses three interaction paradigms. The first paradigm assessed the physiological and behavioral reactivity of individuals to challenge in a novel environment corresponds to their social role including rank, strength of the individuals dominance (dominance discrepancy), the troop's consensus on individual's dominance (social power), and the diversity of cage mates the individual intervenes in conflict (intervention degree). Therefore, individuals with less behavioral and physiological reactivity to challenging stimuli are predicted to have higher rank, dominance discrepancy, social power, and intervention success within the network. The second paradigm assessed how an individual responds to novel challenge has consequences on their ability to dissipate conflict. Even though all interveners agitate conflict, those with lower physiological response (cortisol) and with more stable personality characteristics are predicted to differentiate dissipaters from non-dissipaters of conflict. The last paradigm examined if individuals in more powerful social roles are better able to manage social aggression as retaliation is less likely to occur. Individuals with higher rank, social power, dominance

discrepancy, and intervention degree are predicted to distinguish dissipaters from non-dissipaters of conflict.

Though this information was collected on a translational biomedical research breeding colony of rhesus macaques, the methods used and knowledge gained may be applicable to the management of social species in zoos, marine parks, and sanctuaries with marginal changes. Additionally, these methods and subsequent manipulations can be tested on this large breeding colony without the potential detrimental effects (e.g., trauma) on zoological populations which are more sensitive to perturbation. Several software packages are available to animal managers for exploring social network structure, calculating matrices, and conducting analysis, however an aim of this study was to identify individual traits which could inform thumb-nail personality assessments. By examining the similarities in connections among personality traits in a network, the roles and positions of personality within different networks can be identified allowing for the creation and dissemination of meta-network analysis tools which can be assessed and employed by zoological population managers.

III. METHODS

3.1   Data Collection

Animals were maintained at the CNPRC, a facility approved by the American Association for the Accreditation of Laboratory Animal Care. No changes were made to routine husbandry or care during observation or assessment. Subjects were given water

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ad libitum and commercial monkey diet, supplemental fresh produce, and all other rationing twice per day per standardized institutional protocols. All occurrences of illness of injury among study subjects were immediately reported to and treated by the CNPRC veterinary staff, and all efforts were made to ameliorate suffering. All aspects of animal management conformed to the Guide for the Care and Use of Laboratory Animals [National Research Council 2011] and the laws of the United States government. This project was approved by the University of California, Davis Institutional Animal Care and Use Committee, protocol #11843.

3.1.1   *Personality Assessments*

Biobehavioral assessments (BBA) were performed on each subject to characterize temperament, emotionality, and behavioral and physiological responsiveness to novel environments. BBA are dimensional analyses of behavioral and physiological responsiveness in individual rhesus monkeys, which are composed of both descriptive ratings and behavioral coding under six testing conditions in a novel environment (Capitanio et al., 2005; Golub et al., 2009), and data have been used in multiple studies to understand the causes and consequences of variation in behavioral responsiveness [Capitanio et al. 2005; Golub et al. 2009; Rommeck et al. 2011; Vandeleest et al. 2011]. Cohorts of 2-4 animals were transferred from their outdoor social groups (see Section 3.1.2) into standard, stainless steel laboratory cages (60cm x 65cm x79cm, Lab Products Inc., Maywood, NJ) for assessment on the morning of the day of testing and returned to their field cage after the completion of training 25-hours later. Subjects were provided *ad libidum* water and Kool-aid™ drink, commercial monkey diet, and fresh fruit. Five to

eight individuals were tested at the same time, comprising a single cohort. Subjects

received the same standardized battery of tests designed to characterize the organization

of behavior and physiological responses to novel and provocative stimuli. The

biobehavioral assessment comprises six tests, each of which was video recorded, during a

25-hour testing session. Five of the six tests were used in this assessment:

1. Behavioral observations in assessment cage. Observations to assess the effects of

   social separation and relocation were conducted by a live observer for 5 minute

   periods once at the beginning (Day 1) and once at the end (Day 2) of the 25-hour

   relocation period using a predetermined random order. An experienced observer

   sat 2.6-meters from the assessment cage and recorded data using the Observer

   software (Noldus Information Technology 2001). Behaviors recorded reflect

   activity states (lie, crouch, locomote), and events including self-directed

   behaviors, vocalizations, facial gestures, and environmental exploration (Table 1).

   Due to slight variations in time, measures were converted to a proportion of the

   total observation time, and the frequencies of states and events were converted to

   rates.

2. Video playback. Animal's responsiveness to social stimuli was assessed through

   presenting the animals with a color video playback of an unfamiliar male rhesus

   macaque displaying neutral nonsocial and viewer-directed aggressive behavior.

   Video playback presents a standardized social stimulus to which rhesus macaques

   readily respond. The 10-minute test session was video recorded and later scored

   using Observer software. Behaviors recorded reflect activity states (lie, crouch,

locomote), and events including self-directed behaviors, vocalizations, facial gestures, and environmental exploration (Table 1). In addition, position (facing front or back of assessment cage) and gaze (subject's eyes directed at or any direction 45 degrees around the video monitor or looking away from the monitor) were recorded.

3. Human-intruder test. The animal's responsiveness to a novel human under standardized and graded conditions of challenge was assessed. A technician (i.e., intruder) sat in profile to the assessment cage approximately 1-meter away for 1-minute (trail designated profile far). Next, the technician moved within 0.3-meters in profile for 1-minute (trail designated profile near). Following, the technician move to the 1-meter mark and faced the assessment cage attempting to maintain eye contact for 1 minute (trail designated stare far). In the last trial, the technician remained in eye contact with the subject and moved to the 0.3-meter mark for 1-minute (trail designated stare near). The 4-minute test session was video recorded and later scored using Observer software. Behaviors recorded reflect activity states (lie, crouch, locomote), and events including self-directed behaviors, vocalizations, facial gestures, and environmental exploration (Table 1). Additionally, the animal's location in the cage (which corresponded to near or far from the intruder) was also scored.

4. Response to novel object. Subject response to a small plastic hollow cylindrical object, approximately 4cm x 9cm containing an Actiwatch sensor. The first object was black in color and was present in the cage when the individual arrived the

first day of testing. The object was removed the afternoon of the first day and was replaced with a second object that was white in color. The Actiwatch (Koninkijke Philips Electronics, N.V.) sensor measured the amount of force exerted on the object when it was manipulated by the subject.

5. Temperament ratings. Technicians performing all tests and animal maintenance rated the overall temperament of each animal during the 25-hour test period. A Likert scale of 1-7 (1 reflecting total absence, 7 reflecting extremely large amount of the behavior) were offered for a list of 29 adjectives describing affect quality. These ratings provide an overall assessment of each individual's personality.

6. Blood Sampling. Three blood samples were drawn from each individual at three time points during the BBA procedure to assess plasma cortisol concentrations. The first sample (1 ml) was taken after the first Holding Cage observations approximately one and a half hours after relocation. This sample reflects the initial response to relocation to the holding cage and is consequently represents a 'stressed' value of cortisol. The second sample (0.5 ml) was taken two hours after the Human Intruder Test approximately seven hours after relocation and reflects the level of daily habituation. Directly after the blood draw, each animal was given an intramuscular injection of dexamethasone (500 ug/kg) to measure the response of the hypothalamic pituitary adrenal (HPA) system, particularly adrenocorticotropic hormone (ACTH), a cortisol-regulating hormone. The dexamethasone suppression test is a standard clinical test which suppresses cortisol output by the adrenal cortex to measure negative feedback regulation of

the HPA system. The third sample was taken after the second Holding Cage observation approximately 24-hours after relocation and reflects the overnight dexamethasone suppression test. All blood samples were drawn into unheparinized syringes and immediately transferred to EDTA tubes. Samples were centrifuged at 4°C at 3,000 RPM for 10 minutes. Plasma was pipetted stored at -80°C until assayed by the CNPRC's endocrine Core Laboratory using radioimmunoassay.

Table 1. Behavioral Ethogram for Biobehavioral Assessment

Behavior	Definition
States:	*frequency and duration*
Sit	hindquarters on perch or floor, includes shifting weight
Lie	relaxed posture with body resting on horizontal surface
Stand	torso in a stationary position and weight supported by at least 3 legs, includes steps taken by only 1 or 2 feet
Active	whole body movement; step, jump
Crouch	ventral surface close to floor, head at or below the level of the shoulders
Sleep	eyes closed
Rock/Sway	unbroken rhythmic movements of the upper body while the animal is sitting or standing
Hang	holding onto ceiling or front mesh; all 4 limbs off floor

Pace	movement back and forth repeatedly covering same route/pace
Motor stereotypy	repeated movement with head or body
Events:	*frequency only*
Scratch	common usage
Self-clasp	hand or feet closed on fur or some body part
Self-bite	discrete biting action, usually directed at limbs and often accompanied by threat face
Suck	insertion into mouth of fingers, toes, or other body part
Self-manipulate	pulling, tugging, or pushing at self, includes masturbation
Self-groom	using hands or lips to pick through or part of hair
Back flip	tossing the body up and backwards in a circular motion in the air
Cage Shake	holding onto cage and shaking it, generating a lot of noise
Coo	medium-pitched, moderately intense, clear "coo" call
Screech	intense, high pitched vocalization
Bark	gruff, abrupt, low-pitched vocalization
Grunt	low chuffing vocalization
Other Lipsmack	other vocalizations not previously described
Threat	scored with at least two or more of the following: open mouth stare, head bob, ear flaps, bark vocalizations
Grimace	exaggerated grin with teeth showing

Yawn	wide open mouth displaying teeth
Tooth Grind	loud gnashing of teeth
Explore	discrete manipulation by hands or mouth with the physical environment or object in the cage
Present rump	rigid posture with rump and tail elevated and oriented toward another individual (often preceded by a look and a vocalization)
Present groom	intentionally presents part of body, freezes in the position for a few seconds, and glances at or tries to get other's attention
eat	common usage
drink	common usage

3.1.2   Social Network

Individual measures derived from established social networks were used from an ongoing program of social network analysis aimed at understanding the internal (group composition) and external (management) factors which contribute to patterns of deleterious social aggression in established multi-male multi-female social groups (80-200 individuals) of rhesus monkeys at the CNPRC. Data collection was conducted from June 2008 through December 2009 (~1400 hours) on seven rhesus macaque social groups (69 total matrilines, 108-197 individuals per social group). All subjects were maintained in large, established social groups in half-acre (0.2 ha) outdoor enclosures to provide for their well-being and normalized behavior. The methodological approach was purely

observational. All enclosures were similar with ten A-frame housing structures, multiple suspended barrels, swings, and multi-tier perching. Rhesus macaques in this outdoor colony were managed with a minimal level of disturbance, which generally included daily monitoring checks, two yearly health examinations on all animals, and removal of injured or sick animals for medical treatment. Individuals of each group were free to interact at will.

Data were collected using event or scan sampling for 6 hours per day, 4 days per week for 1 week during each group's study period, yielding 6 weeks of observations (~144 hours) per group. Data were collected on affiliative (e.g., groom, reconcile, huddle, rump, present), submissive (e.g., move away, run away, scream, silent bared teeth display, rump present), and aggressive interactions (e.g., threat, chase, bite) among individuals in each group comprising 112,189 event samples (conflict, status signaling, reconciliation) and 24,621 scan samples (grooming, huddling) in the data set. Inter-observer reliabilities had a mean of 91% agreement across three observers (SD = 0.03; range 0.86-0.94; kappa – 0.65, $p<0.0001$). Data were also collected for group attributes, such as group size, proportion of different age/sex classes, number of matrilines, sex ratio, size of matrilines, mean kin coefficients (average matrilineal degree of relatedness), trauma (number of wounds requiring hospitalization), and social relocations (number of animals permanently removed from group due to extreme aggressiveness or targeted aggression).

3.1.1   Subject Selection

In each of the seven social groups, 36 individuals identified from the social network dataset (see Section 3.3.1) were selected based on the count of successful third-party interventions in non-kin conflicts. Each animal was given a dissipation score and an agitation score. The dissipation score was assigned based on a count of successful interventions on non-kin conflicts based on the following criteria: (1) previous conflict stops, (2) intervention aggression was unknown (i.e., data were sparse) or brief, or (3) all conflict stops. Individual entropy scores were determined from the count of diverse intervention targets and allies. The two entropy values were summed so that each individual received a single score based on the diversity of targets and allies of their successful interventions. Impartial interventions could not be included in entropy scoring since there was no clear target or ally; therefore an additional 0.5 points were given to each individual with a successful impartial intervention. Total scores were then divided by the total observation time on that individual to yield equivalent data sets for each individual. High scores mean that an individual has a high number of successful interventions on non-kin conflicts or a high diversity of non-kin targets and allies.

An agitation score was assigned based on the total duration of conflict initiated by an individual, i.e., the duration of all fights initiated by an individual were summed over the entire data period. This duration was then divided by the total observation time that an individual was present to yield equivalent data sets for each animal. Animals with the highest scores started fights with long duration. Animals were then assigned an agitation rank based on this measure, with the animals with the highest agitation score given the highest rank.

Since animals may fail in their attempts to stop conflict, many dissipaters in the dataset were also agitators. Therefore, agitators were chosen based on a combined agitation/dissipation score. An animal was said to be an agitator if they had a high agitation rank relative to their dissipation rank. The top three animals with the highest difference were chosen as dissipater. For each cage, the top three dissipaters and top three agitators with no dissipation score (hereafter, non-dissipaters) were selected for BBA assessment. Dissipation was then converted to a dyadic measure for assessment (0 = non-dissipater, 1 = dissipater).

3.3   Data analysis

3.3.1   Biobehavioral assessment

1. Holding Cage Observations. Previous factor analyses conducted on holding cage observations with infant rhesus macaques showed differences in two factors, Activity and Emotionality (Capitanio et al., 2005; Golub et al., 2009). As similar factors would be informative to the nature of dissipation, an exploratory factor analysis was conducted on the holding cage data set. Behaviors with less than 2 observations were removed from the data set due to their low occurrence resulting in a remaining data set of 19 measures for each day (duration: crouch, locomote, sit, sleep, stand, active; frequency: cling, crouch, environmental explore, eat, grimace, locomote, lip smack, self groom, sit, sleep, stand, threat, vocal 'coo'). Because some variables were skewed (high proportion of zero-scores), data was dichotomized (1 = displayed, 0 = not displayed). Exploratory factor analysis was

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then performed on the resulting data set using weighted least squares with robust standard errors for extraction of factors. The items were then rotated (promax) and assessed for factor consistency. Based on the small number of subjects and the number of items loading into the model (19 items), confirmatory factor analysis was not possible. In this case, Chronbach's-α (range = 0.6-0.8) was used as a multivariate approach to determine patterns of correlation among each variable and to maximize internal consistency (Capitanio et al., 2005; Cronbach, 1951; Golub et al., 2009). From these analyses, factor scales were not able to be produced due to conformability errors (a result of limited or no variability). Following this, an exploration of the original data set using the Activity and Emotionality factor loading scales identified for infants in BBA was then attempted. However, as adults do not display the diversity of behaviors infants do, only three (duration of locomote, dichotomous variable for crouch, dichotomous variable for eat) of the original six factor loadings in Activity and three (dichotomous lip smack, dichotomous variable for threat, rate of vocal 'coo') of the original five factor loadings in Emotionality were robust enough to assess, and as such were not representative of the original scales. Data from holding cage observations were therefore not included in future analysis.

2. Video playback. It was anticipated that some individuals maintained a latency to react to the video of the aggressive conspecific. Assessment was therefore conducted to identify a possible threshold effect in reactivity to social (threatening) stimuli. Durational data were aggregated such that each individual

received one total duration score for each condition (non-aggressive or aggressive conspecific) in each of the three paired trials. The binary outcome of dissipation was assessed using logistic regression for duration of activity, duration of time looking at or away from the video monitor and position (front or back of the cage) and accounted for each individual as a repeated measure. Each of the six conditions were of variable length due to the amount of behavior exhibited, thus condition duration was included in the models as an exposure variable.

3. Human-intruder test. Data were aggregated with the duration of behavior occurrence converted to the proportion of time observed and the frequencies of behavior occurrence converted to a rate. The binary outcome of dissipation was assessed using logistic regression for positional (back of the cage, front of the cage) and behavioral (active, explore, grimace, sit, stand) effects. A nested random effect of home cage was included to account for discrepancies between home cages. Likely due to the scarcity of the data set there were no significant predictors of dissipation. Following this, exploratory factor analysis was attempted using the same methodology described in Holding Cage Observations to combine data for robustness. Factor scales were not able to be produced due to conformability errors. Data from the human Intruder Test were therefore not included in future analysis.

4. Response to novel object. Due to the small amount of interaction with the novel object, predictive models were not able to be assessed.

5. Temperament ratings. Previous factor analysis conducted using adjective descriptors of temperament with infant rhesus macaques showed four factors: Bold, Excitability, Equability, and Warm (Golub et al., 2009). As similar factors would be informative to the nature of dissipation, an exploratory factor analysis was conducted on temperament scales for this study. Similar to test cage observations, ratings on each adjective descriptor were assessed by exploratory factor analysis of the adjective descriptors using weighted least squares with robust standard errors. The items were then rotated (promax) and assessed for factor consistency. As these data are considered distributed continuously, maximum likelihood was used as a method of estimation of fit criteria. As in the above factor analysis, the small sample size compared to the number of descriptor loadings did not allow for confirmatory factor analysis. Chronbach's-α (range = 0.6-0.8) was again used to determine patterns of correlation among each variable and to maximize internal consistency. From this analysis, scales were able to be constructed and were used in further analysis.

6. Cortisol. Cortisol and measures of innate immunity can act as measures of a subject's physiological responsiveness to a novel and challenging environment (i.e., stress). Measures of innate immunity (white blood cells, neutrophils, monocytes, and lymphocytes) were assessed from the first blood sample using Poisson regression and included a nested random effect of home cage to account for discrepancies between home cages. As hematological samples were taken at three time points, analysis was conducted to observe overall changes in cortisol as

well as habituation. Two models of cortisol were assessed using Poisson regression and included a nested random effect of home cage to account for discrepancies between home cages. The first assessed changes in overall cortisol as a result of being a dissipater. The second assessed changes in cortisol as a result of being a dissipater in each of the three samples.

3.3.2 *Social network analysis*

To address the effects of the novel challenge (temperament and hematology) on social roles, individual-level network measures of social power, dominance discrepancy, and intervention success were assessed. Social power and intervention success were assessed as positive continuous measures using Poission distribution. Dominance discrepancy was assessed using generalized linear models with a Gaussian distribution due to the presence of negative values. Home cage was included as a repeated measure in each model to account for discrepancies between network measures.

Network measures were also used to statistically examine the association between the binary variable of dissipater and individual network measures using logistic regression models. Home cage was included as a repeated measure in each model to account for discrepancies between network measures. Network measures used in this analysis and their definitions are included in Table 2.

3.3.3 *Statistical analysis*

Statistical models were compared using the following criteria: insignificant model terms (p<0.08, unless otherwise noted) were excluded from the model and models having a difference in AIC less than or equal to two were considered equivalent [Burnham and

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Anderson 2002]. Statistical analyses were conducted in Stata 11 (Stata Corp, College

Station, TX).

Table 2. List of Measures and Operation Definitions Used in Analysis

Term	Definition
Corporative Rank	Social rank of each individual within the cage accounting for matrilineal hierarchy (Fushing et al 2011)
Social Power	First-order entropic measure of the number of individuals from which an individual receives subordination signals as well as the number of subordination signals received (McCowan et al. 2008, 2011)
Dominance Discrepancy	Incongruity in dominance of one individual to others in the group as measured by the receipt of submissions singals than what is expected
Intervention Degree	Diversity of individuals on which an individual initiated interventions whether successful or not (McCowan et al. 2011)
Reconciliation Reciprocity degree	Diversity of individuals from which an individual receives reconciliation through grooming (McCowan et al. 2011)
Grooming Received degree (weighted)	Measure of the number of individuals from which an individual receives grooming as well as the number of grooms received
Grooming Betweeness Centrality	Potential of individual to maintain group cohesiveness as measured by the shortest paths linking every pair of individuals in the network (McCowan et al. 2011)

IV. RESULTS

4.1   Dissipater demographics

A higher proportion of males were identified as dissipaters (males = 0.72) than

non-dissipaters (males = 0.11). Likewise, only two males were identified as non-

dissipaters. A high correlation between the binary predictor of dissipation and sex exists

in this dataset; therefore, it was not possible to delineate sex effects in models without

colinearity Of the 13 adult males identified as dissipaters, three were unrelated.

4.2 Reactivity to Novel Challenge

4.2.1 Video Playback

Dissipaters can be distinguished from other interveners by non-reactivity to

stressful social situations and their awareness of threatening conspecifics. During the

aggressive condition, dissipaters were less active ($\beta = -0.372$, $P < 0.001$), spent less time

in the back of the cage ($\beta = -0.368$, $P < 0.001$) and spent more time with their gaze

directed towards the threatening conspecific (looking away from the monitor: $\beta = -0.327$,

$P = 0.014$). No clear threshold effect could be identified as no differences were seen

between the first and third aggressive trials. However, in the second aggressive trial

dissipaters were less active ($\beta = -0.0335$, $P = 0.017$), spent less time in the back of the

cage ($\beta = -0.368$, $P < 0.001$), and spent less time looking at the monitor ($\beta = -0.458$, $P <$

0.001). The subjects did not show enough aggressive (threat, lunge) or displacement

(scratch self, cling, environmental explore) behaviors to be assessed, even when

aggregated into categories, suggesting that these video stimuli may not be salient enough

to elicit responses from adult interveners as a whole.

4.2.2 BBA Temperament Scales

Three factor scales were identified based on best fit factor loadings (Chronbach's

$\alpha = 0.83$) for third-party interveners and which were labeled Bold, Gentile, and Restless

based on highest loading item in each scale (see Table 3 for adjective loadings, definitions, and Chronbach's alpha per scale). Varimax rotation produced very similar factor patterns. The label for Bold and Gentile scales were derived from the highest positively loading adjective descriptor which described the other composite loading items. For the factor scale labeled as Restless, the highest loading item, Active, did not describe the other loading items (playful, nervous, and not slow), when taken in the context of adults in a novel environment. This scale is more likely descriptive of anxious or displacement-type behavioral patterns. Dissipaters were no more Bold or Gentile than non-dissipaters, but were less Restless (β = -0.147, P = 0.032).

Table 3. Personality Dimensions in High-intervention Macaques in a Novel Environment

Trait:	Bold*	Gentile*	Nervous*	Trait description:
active	0.1428	0.1037	**0.9245**	- moves about a lot, not lethargic.
aggressive	0.2161	**-0.9536**	-0.0304	- high frequency of displays, threats.
bold	**0.9592**	-0.1243	-0.0205	- is daring, not restrained or tentative. Not timid, shy, or coy.
calm	0.3553	**0.6751**	-0.3547	- reacts in an even, calm way; is not easily disturbed. Not agitated. Restful, peaceful.
confident	**0.9341**	-0.0251	-0.1433	- behaves in a positive, assured manner, not restrained or tentative.
curious	**0.6036**	0.1298	0.2910	- readily explores new situations, seeking out or investigating novel situation.
flexible	**0.5359**	0.2375	0.0460	- adapts to situations. Is able to accommodate new ways of doing things.
gentle	0.0361	**0.8618**	0.1034	- subject responds to technicians in an easy-going, kind, and considerate manner. Subject is not rough or threatening.
irritable	0.2106	**-0.8449**	-0.0555	- reacts negatively with little provocation.
nervous	-0.2848	0.0879	**0.5523**	- jittery, seems to be anxious about everything.
playful	0.1271	-0.0356	**0.8384**	- engages in self-play (hanging, swinging, jumping) or object play.

slow	0.2338	0.2531	**-0.6776**	- moves and sits in a relaxed manner; moves slowly and deliberately, not easily hurried.
tense	**-0.6958**	0.1455	-0.2244	- Shows restraint in posture and movement; carries the body stiffly, which suggests a shrinking tendency, as if trying to pull back and be less conspicuous.
timid	**-0.8831**	0.1206	0.0091	- Subject is easily alarmed and is hesitant to venture into new situations.
vigilant	**0.7360**	0.1011	0.2386	- Ready, attentive, watchful, notices with special attention. Not oblivious to surroundings.
Eigenvalue	4.80875	3.49342	2.06341	
Proportion	0.4639	0.337	0.1991	

Chronbach's alpha = 0.8298.
*Scale values displayed are factor loadings from promax rotation.
Values above 0.6 are bold type and indicate items which best load in each factor scale.

4.2.3 Cortisol

There were no statistical differences in overall cortisol between dissipaters and nondissipaters. However, non-dissipaters showed a 30% higher cortisol concentration in the first blood sample (Fig. 1), which was significant (dissipater: mean = 45.158, SD = 34.340; non-dissipater: mean = 75.376, SD = 15.163; β = -0.089, P = 0.052). Later samples showed no difference between dissipaters and non-dissipaters, suggesting the initial activation of the HPA axis in response to an unfamiliar environment differentiates third-party interveners.

No differences were seen in white blood cell counts in the first sample suggesting stress levels were acute and likely not a result of differences in capture time or methods of transport from home cage to the testing room. However, differences between

dissipaters and nondissipaters were seen in two measures of innate immunity (monocytes: $\beta = -0.072$, $P < 0.001$; lymphocytes: $\beta = -0.446$, $P < 0.001$). Regardless, direct correlation between cortisol and immune measures were not significant.
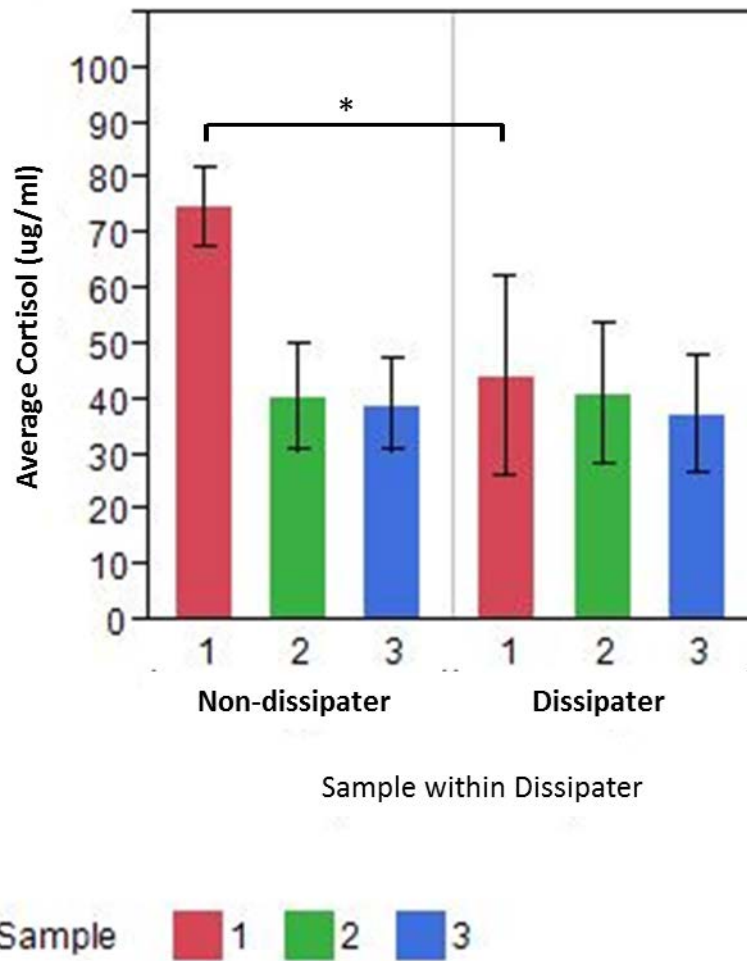
Figure 1. Three samples of cortisol drawn in a novel, challenging environment from dissipaters and non-dissipaters of social conflict. Samples were taken 2-hours, 7-hours, and 24-hours after removal from home cage.

4.3   Influence of Social Roles

4.3.1   Reactivity to Challenge and Social Role

Similar patterns of interaction were observed between BBA-derived temperament scales and the social roles these interveners exhibit in their home cages. Individuals with higher social power and intervention degree were more bold (social power: $\beta = 0.095$, $P < 0.001$; intervention degree: $\beta = 0.022$, $P = 0.005$) and gentile (social power: $\beta = 0.087$, $P = 0.003$; intervention degree: $\beta = 0.047$, $P = 0.005$) but less restless (social power: $\beta = -0.069$, $P = 0.005$; intervention degree: $\beta = -0.057$, $P < 0.001$). Individuals with more dominance discrepancy were more gentile ($\beta = 1.091$, $P = 0.050$), but did not show any differences in boldness or restlessness. The effect of cortisol was lower in both social power (overall: $\beta = -0.019$, $P < 0.001$; sample 1: $\beta = -0.321$, $P = 0.002$) and intervention degree (overall: $\beta = -0.005$, $P < 0.038$; sample 1: $\beta = -0.010$, $P = 0.084$) but higher for dominance discrepancy (overall: $\beta = 0.983$, $P = 0.050$; sample 1: $\beta = 946$, $P < 0.001$).

4.3.3   Social Role and Conflict Management

Two models were shown to be equivalent based on model selection criteria (see section 3.3.3) in describing what social roles predict dissipation. First, more social power ($\beta = 0.560$, $P = 0.049$) and higher intervention degree ($\beta = 0.526$, $P < 0.001$) lead to strong prediction of dissipation (AIC = 23.624). Second, higher dominance discrepancy ($\beta = 2.102$, $P = 0.039$) and intervention degree ($\beta = 0.257$, $P < 0.001$) also predict

dissipation (AIC = 22.580). From this, an individual's rank did not contribute to the likelihood of dissipation as models including rank as an effect were either higher in AIC or the term was insignificant. Though social power and dominance discrepancy measure different aspects of an individual's social role, they are both calculated using the number of subordination signals received per individual, and likewise contributing to them being including in similar models. Regardless, in comparing two models of intervention degree, dominance discrepancy was more predictive ($\beta = 0.215$, $P < 0.001$) than social power ($\beta = 0.035$, $P < 0.001$) as evidenced by the stronger coefficient and lower model selection parameter ($\Delta AIC = -24.79$).

V. DISCUSSION

Aggression is used by both male and female rhesus macaques to establish and reinforce social position [Lindburg 1971]. The degree to which individuals utilize personality and aggression to not only gain position but fit a particular social role is not well understood, but is believed to be due to more than the summation of winning outcomes in previous conflict. This study demonstrates that some individuals play an important role in dissipating social conflict due to their reactivity to novel situations, interconnectedness to their group, power and rank dynamics, and temperament.

5.1   Response to Novel Challenge

How an intervener reacts to challenging situations, both behaviorally and physiologically, is an important component to the successful outcome of dissipating

aggression. While all interveners can aggravate conflict through intervention, those that dissipate are distinguishable from other interveners by non-reactivity to stressful social situations and their awareness of threatening conspecifics. Though this assessment could not determine differences in reactivity thresholds (i.e., when interveners become aware of a threatening conspecific), dissipaters appeared more prone to recognize if a threatening conspecific is a true risk. During the Video Playback assessment, non-dissipaters directed their attention away from the monitor in the aggressive condition during the second trial, which suggests they may have some degree of awareness that the threatening conspecific is of moderate to no true risk. Regardless, the degree of agonistic response is negligible in this case as none of the interveners displayed enough aggression toward the monitor to be able to be assessed. Because of this, social competency in determining risky versus nonthreatening social situations may be a characteristic of interveners as a whole.

Seemingly more important is the personality of the intervener as assessed in a novel, challenging environment. Complimentary patterns were seen in the temperament factor scales derived in this assessment with those using the same adjective descriptors in normal social situations [see Capitanio, *et al.* 1999; McCowan, *et al.* 2011]. Combined, these studies show that individuals engaging in third-party intervention tend to be bolder, more sociable, and less aggressive. This study adds two important aspects to this literature. First, because similar patterns emerge when interveners are confronted with challenge in a novel environment, there is increased evidence for the consistency of these trait ratings and their manifest patterns. Specifically, boldness and gentleness appear to be personality characteristics which can be assessed in both stressful, novel environments as

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well as in more naturalistic settings, and distinguish conflict dissipaters under both conditions.

Second, though boldness and sociable temperaments have previously been associated with higher social power and intervention success [McCowan *et al.* 2011], this assessment showed that dissipaters can be further distinguished from their intervener counterparts in regards to their diminished propensity for anxiousness when confronted with novel challenge. Though the temperament scale of restless (active, nervous, playful, and not slow) at first appears to suggest these individuals could be described as cautious but engaging, in the context of a challenging and stressful environment, descriptors such as play and active are more descriptive of displacement-type behaviors. Displacement activities have been described as self-directed behaviors which arise in situations of social tension and anxiety [Troisi 2002]. As dissipaters are characterized by decreased arousal in such stressful situations, they are better prepared to engage and navigate the complex social dynamics which compose an intervention. This is further exemplified in that dissipaters are characterized by factor loadings of bold, calm, confident, and not tense.

These temperament outcomes were consistent with physiological responses to novel challenge as well. Under stressful situations, dissipaters tend to respond more calmly both behaviorally and physiologically. The activation of the HPA axis seen in the first blood sample exhibited the greatest difference in responsively between dissipaters and non-dissipaters; however the ability for non-dissipaters to habituate to

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physiologically similar levels of stress in later samples typifies the adaptability of the rhesus macaque. Given the bi-directionality of the immune measure coefficients, other factors in addition to stress may be influencing immune function in these animals that were not able to be identified with this data set. Regardless, the higher level of cortisol in non-dissipater's first sample demonstrates that these individuals do react differently to stress. Unfortunately, initial behavioral assessments and acute immunological measures were inconclusive but could have provided a much more comprehensive picture of how interveners react to stress. In turn, stress-related reactivity may influence how an individual responds to unpredictability in complex social situations, such as the outcome of intervention, and therefore may influence the individual's ability to manage conflict. These aspects would benefit from additional investigation.

5.2   Social Position of Conflict Managers

How individuals respond to challenge in a novel situation maintains symmetry to their ability to manage the social environment as well. Rank, social power, and power discrepancy are all measures of social status and an individual's competitive ability. Rank contributed disproportionately low in comparison to other measures of dominance. An important outcome is suggested as rank is calculated based on wins of aggressive conflict where other measures of competitive ability (i.e., social power and dominance discrepancy) utilize measures of subordination signaling in their calculations. Because dissipaters receive more unsolicited subordination signals, they reside in more secure positions and tend to not have to use aggression to solicit signals of subordination.

Dissipaters were therefore less likely to have an intervention contested, decreasing the likelihood of an intervention which aggravates a conflict.

Power discrepancy represents the variance amongst dominance relations within a group, and similar to social power, individuals with high discrepancy do not need to engage in aggression since there is little contest of their status. Likewise, individuals with high dominance discrepancy are seen as conflict managers within their groups as they tend to intervene and dissipate aggressive conflict. This study aligned with the patterns that the more dominant an individual the more likely they were to intervene successfully in conflict. From this, it may not be the engagement of winning of previous conflicts that predicts the ability of an intervener to dissipate conflict but the agreement of the troop, as evidenced by subordination signaling. Lastly, because dissipaters were shown to have a high intervention degree, they were likely to be more successful in a diverse number of interventions. In other words, dissipaters were more effective at managing conflict across a group as a whole compared to non-dissipaters. Because there was much social group agreement in the social position of dissipaters, it was not surprising that they were the highest ranking interveners.

Because dominance discrepancy maintained a stronger relationship with the diversity of individuals one intervenes with, those agitating conflict were doing so with fewer individuals with similar dominance. Because non-dissipaters were disproportionately female, an interesting, but unsurprising pattern may be present which suggests that female's intervening in conflict were likely driven to assist an involved

party rather than to dissipate conflict. Unfortunately, it was not possible with this data set to parse kinship or alliance relationships between intervener and conflict aggressor to further address this question. Additionally, due to the highly sex-biased nature of this data set, it was not possible to delineate sex effects from the binary predictor of dissipation without colinearity due to the high correlation between the two variables. Because of this, future studies should seek to differentiate or account for male and female intervention outcomes as they are likely served by different social processes and roles in conflict management.

5.4   Implications for *Ex-situ* Population Management

These results demonstrate that individual personality and group interconnectedness play a fundamental part in defining the social roles individuals play in managing aggression. Because dispersal of captive groups is mediated by humans, it is important to understand not only the overall natural pathways which mediate dispersal, but also how animal management activities may disturb these natural pathways. In ongoing investigation of deleterious social aggression in large rhesus macaque groups, McCowan and colleagues have identified three major pathways which negatively influence social stability: (1) matrilineal genetic fragmentation, (2) presence of natal males, and (3) decreased social power [Beisner et al. 2010; Beisner et al. 2011a; Beisner et al. 2011c; McCowan et al. 2011]. The presence of natal males is unique to *ex situ* population management as these individuals are inhibited from disbursing from their natal groups. Natal males are more likely to gain from kin-alliances the longer they

remain in their natal groups, particularly when they belong to a high ranking matriline [Beisner et al. 2010]. These males also use aggression more frequently and when removed, intense aggression within these groups is reduced. In short, the absence of natural dispersal in these populations can be a cause for concern as genetic relatedness, age and sex characteristics, and natal alliances additionally contribute to conflict [Beisner et al. 2010; Beisner et al. 2011a; Beisner et al. 2011c; McCowan et al. 2011].

The results of this study also showed that females had a role in agitating aggression. This pathway is tied to dominance and group stability but is likely separate based on the *intent* of the intervener. Females were more likely to intervene on conflict to aid an aggressor within their own matriline, where this was less likely in non-natal males. The focus of intervention has historically been on outcomes, i.e., aggravation or dissipation of conflict, and intervention type, i.e., impartial or directed intervention. Beyond sex and partiality of the intervener, a better understanding of kin-biased intervention, diversity and power dynamics of matrilines, and males alliances would help to enhance predictability of not only the outcome of intervention but in identifying the individuals most likely to dissipate conflict. These aspects are important not only in understanding group dynamics of aggression (i.e., identifying the type of conflict each sex is likely to agitate or dissipate), but in determining how different types of intervention influence the cascade of aggression and consequential group-level outcomes such as group stability. By understanding these dynamics and having the ability to identify individual contributions to group stability, population managers could employ better informed decisions in managing animal populations.

5.5   Conclusion

This study sought to identify characteristics of individuals who successfully intervene on intergroup conflict and manage group aggression based on the social roles, temperament, and reactivity to novel challenge. The intent was to take another step towards the creation of meta-network analysis tools which can be employed by population managers to manage deleterious aggression. The results showed that among rhesus macaques, conflict dissipaters differed from other interveners because they were posed to behaviorally and physiologically cope better with the stress of unpredictability. This study also demonstrated that specific social roles were multifarious: individual attributes influenced an individual's ability to engage in conflict management, but how the group agreed on the dominance status of that individual also contributed to a successful intervention. Lastly, this study suggested that males and females engaged in intervention for different reasons. Males engaging in conflict appeared to play a role in dissipation, whereas female engagement in non-kin conflict was seemingly more complex and requires continued investigation.

From a population management perspective, an inappropriate sex ratio has important implications to the reproductive success of *ex situ* social species [Kleinman 1994a; Lyndburg and Fitch-Snyder 1994; Moberg 2000; Stobbkof 1983] beyond simple assess to potential mates. Due to their prominence and facilitative characteristics, dissipaters play a key social role in affecting network cohesion – an aspect which transcends our study species. Removing such individuals distracts from population

management goals, as reproduction decreases as conflict rate increases [see Kleinman 1994b]. This study took another step towards clarifying the roles and positions of individuals within different networks, though more investigation is needed in two main areas. For rhesus macaques in particular, identifying female roles in the dissipation of non-kin conflict is little understood and likely effects social group stability through different mechanisms than that of males. Second, similar studies need to be conducted in non-macaque species to understand how meta-network analysis tools can be tuned to different social group paradigms if tool is to be useful and employed by zoological population managers.

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CURRICULUM VITAE

Darren Minier's focus is to enhance welfare and conservation management of captive animals through effective application and applied research of animal behavior management techniques. He is currently a research specialist in the McCowan Animal Behavior Laboratory for Welfare and Conservation at the University of California, Davis. He has spent the past 10 years working with zoos, sanctuaries, marine parks, laboratories, and academic institutions in California, India, and Africa. Concurrently, Darren received three degrees from the Exotic Animal Training and Management Program at Moorpark College in 2002 and his BS in Wildlife Conservation Biology and Behavioral Ecology from the University from California, Davis in 2009.

Darren is thankful to have had the opportunity to work with a large range of taxa in different aspects of husbandry and behavior management. Over the last several years, he has had the opportunity to assist in building training and enrichment programs in small zoos, laboratories, and sanctuaries – both nationally and internationally- through consultation. Darren currently coordinates collaborative behavioral investigations and monitoring programs with several zoos and marine parks.

Darren is dedicated to professional service, and has been a member of AZA for over 10 years. He is a board member of the Animal Behavior Management Alliance, and is the Chair of the Research and Evaluation Committee and the 2012 Conference Committee. He is also sits on the board of the Moorpark College Foundation, and Chairs the development of the Friends and Alumni of America's Teaching Zoo. Darren serves on the Captive Care Committee of the International Primatological Society, the Animal Behavior Society's Animal Care Committee, and the Executive Review Committee for the International Primatological Society. Darren served as the founding Director of Animal Care and Welfare for The Peacock Foundation from 2003-2010, an organization committed to animal-assisted intervention for children overcoming grief, loss, or trauma in Los Angeles.