STRANGERS IN A NEW LAND: THE EFFECTS OF ECOLOGY ON FEMALE SOCIAL RELATIONSHIPS, *MACACA MULATTA*, OCALA NATIONAL FOREST, FLORIDA

by

Adam Patrick Johnson

A thesis submitted to the faculty of
The University of North Carolina at Charlotte
in partial fulfillment of the requirements
for the degree of Master of Arts in
Anthropology

Charlotte

2017

Approved by:

____
Dr. Jon Marks

____
Dr. Coral Wayland

____
Dr. Lydia Light

ABSTRACT

ADAM PATRICK JOHNSON. Strangers in a new land: the effects of ecology on female social relationships, *Macaca mulatta,* Ocala National Forest, Florida. (Under the direction of DR. JON MARKS)

Despite the vast research into rhesus macaque (*Macaca mulatta*) social behavior, little is known about how they adapt to novel environments, particularly in cases where they experience little or no between-group competition and are not provisioned. A rhesus macaque population was introduced into Silver Springs State Park (SSSP) in central Florida in the mid-1930s and has spread into the Ocala National Forest. The study group, 14km northeast of the original population in SSSP, along the Dead River experiences no observed intergroup competition, is not provisioned, and has access to abundant and distributed food throughout the riverine floodplain. Rhesus macaques are considered the archetypal species for phylogenetic inertia, an evolutionary adaptation to past ecological conditions, which then produced a static behavioral pattern. Over 231.5 hours of observation during June and July of 2016, the Dead River macaque group was observed to break from the species-typical pattern of high levels of agonism and a steep, stable hierarchy, and instead demonstrated a shallow hierarchy with infrequent agonism in a feeding context. This indicates that rhesus macaques are capable of significantly changing behavior when living under novel ecological conditions. A deeper understanding of the relationship between primate species and their environment is essential to addressing the anthropogenic pressure placed on other species that experience phylogenetic inertia but are also at risk from human encroachment and anthropogenic climate change.

ACKNOWLEDGMENTS

I am deeply indebted to my committee for their unwavering support and encouragement: Dr. Jon Marks, my committee chair; Dr. Coral Wayland; and Dr. Lydia Light. Without you, this project would have never been completed as you kept me focused and grounded throughout my research, despite life throwing everything and the kitchen sink at me. I am so fortunate to have met you; you’ve made me a better anthropologist and a better person.

For all the people that listened to my crazy ideas: Lennin; Amanda. To Dr. Sarah Pollock, for your companionship, emotional support, and help with the dreaded statistics; Dr. Christof Neumann, for helping me understand Elo-rating and R-studio; Dianna, for being the best possible mom for our daughter, giving me peace of mind; and my mother, Susan, for teaching me the value of hard work and passion. Dr. Katie MacKinnon, Dr. Erin Riley, Amy, and Carolyn for helping me finally find my field site.

Finally, I would like to thank my daughter, Amelie, for keeping all the hard work, injuries, and discomfort in perspective. You have been the greatest motivation and inspiration. Without you, I would have never even attempted any of this!

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

DS	David’s score
EMFSR	Ecological model of female social relationships
FSDT	Food-site depletion time
normDS	Normalized David’s score
SSSP	Silver Springs State Parks

CHAPTER 1: INTRODUCTION

Mammals organize into various types of social patterns, from species that have solitary territories (Smith, 1993) to species that form large social groups of varying levels of sociality (Hoeck et al., 1982). Primate taxa reflect this diversity in grouping patterns, and understanding the mechanisms that produce the observed patterns can have broader implications to include conservation. Without the ability to adapt both individual and group behavior to a changing environment, primates run the risk of losing genetic diversity and thus, going extinct (Strier, 2017). Behavioral flexibility provides organisms with a means to rapidly adapt to a changing environment and thus are better equipped to deal with the effects of habitat fragmentation and anthropogenic climate change (Charmantier et al., 2008).

Female defense polygyny, male reproductive defense of females against other conspecifics, has been argued to be the ultimate cause of multi-male multi-female grouping (van Schaik and van Hoff, 1983). This explanation responds to reproductive pressure on males but ignores ecological pressures that 1) act on the females, 2) act on the group as a whole, and 3) do not address behavior variability within species. Ecological models address these issues by examining the effects of the environment, such as food distribution, abundance, and predation pressure on individual behavior and grouping patterns (Koenig et al., 2013). Therefore, different ecological conditions may produce different grouping patterns.

The diversity of grouping patterns among primates is alternatively explained by adaptation to a specific historical environment, which then produced a particular static grouping pattern, a concept termed phylogenetic inertia (Thierry, 2008). As a result, evolutionary closeness is a predictor of grouping patterns with the assumption that species that share a recent common ancestor are likely to have developed their grouping strategy in a common ancestor as an adaptation to the ancestral environment. Thus, some grouping patterns cannot be broken without new, strong selective pressures.

There are two assumptions implicit in the phylogenetic model; 1) grouping patterns are produced by adaptation to an ancestral environment and thus, are biologically determined, and 2) ecological conditions today must be sufficiently similar to ecological conditions that produced the observed grouping patterns as significant changes in ecological pressures would override the phylogenetic inertia and necessitate adaptation. These assumptions preclude any behavioral adaptation to current ecological conditions (Thierry et al., 2000).

According to Isbell's (1991) Ecological Model of Female Social Relationships (*EMFSR*), variation in ecological factors such as the distribution of food, predation risk, and intra- and intergroup relationships (Jansen and van Schaik, 1988; Isbell, 1991; Sterck et al., 1997) is the primary predictor of social organization. When resources are evenly distributed and not easily monopolized, egalitarian groups should form. With high between-group competition, females should demonstrate more philopatric behavior (*Resident-Egalitarian*) and more dispersed behavior (*Dispersal-Egalitarian*) when there is low between-group competition (Balasubramaniam et al., 2014).

When food resources are clumped and defensible, frequency of between-group competition influences social organization. Low levels of between-group competition produce *Resident-Nepotistic-Despotic* groups where philopatric females form steep, stable dominance hierarchies (Balasubramaniam et al., 2012) maintained through intense aggression (Berman and Kapsalis, 2009), with little post-conflict resolution (Demaria and Thierry, 2001). High levels of between-group competition produce *resident-nepotistic-tolerant* groups in which dominant females are more tolerant and thus have a shallower, less stable dominancy hierarchy, engage in less agonistic behavior and more post-conflict resolution (Sterck et al., 1997).

One species that has been demonstrated to organize in a *resident-nepotistic-tolerant* pattern are rhesus macaques (*Macaca mulatta*). In rhesus macaque societies, dominant females monopolize high-quality food-types and thus engage in high levels of within-group competition (Thierry et al., 2004; Thierry, 2007; Balasubramaniam et al., 2014). While rhesus macaques are widespread and seem to retain this social organization across various ecological situations (natural habitats, provisioned, commensally with humans), little is known about how they respond to novel, unprovisioned habitats. Prior studies have examined rhesus macaque social organization in their native habitats, in proximity to humans, or in provisioned groups. A population of rhesus macaques can be found in central Florida, originally inhabiting Silver Springs State Park (SSSP). Here, a group northeast of SSSP (Fig. 5), along the Ocklawaha and Dead Rivers, experience little to no between group competition and are unprovisioned.

Here we have an opportunity to expand our understanding of behavioral plasticity in rhesus macaques and thus provide insight into the types of ecological upheaval to which primates can adapt. The Dead River macaques have little or no between-group competition and food is also distributed throughout the floodplain and not isolated to high quality patches (Monk, 1966). The ecological model predicts that with dispersed feeding sites and little between-group competition, the females should disperse more, resulting in lower frequencies of agonistic interactions and a less stable dominance hierarchy. However, the phylogenetic model indicates that all rhesus macaques should conform to the *resident-nepotistic-despotic* formula due to their evolutionary history. The two models attribute the cause of grouping patterns to different factors and conflict with one another. Intra-species plasticity would confirm *EMFSR* but conforming to the typical rhesus macaque archetype will not necessarily invalidate the ecological model because the *resident-nepotistic-despotic* formula may be a useful pattern in diverse ecological conditions.

The purpose of this study is to evaluate the grouping pattern of an introduced population of free-ranging rhesus macaques (Wolfe and Peters 1987; Gottschalk, 2011; Anderson et al., 2017) in order to answer the question: *can rhesus macaques adapt grouping patterns and social interaction to a novel environment?* In 1937, a group of rhesus macaques were relocated to a hardwood swamp environment with abundant and dispersed food resources in north-central Florida (Monk, 1966). These Dead River macaques serve as an appropriate study group due to their fairly recent introduction to the area, which limits the time in which phylogenetic inertia could be overcome, and lack confounding factors like provisioning and habituation, which introduce new variables that the study subjects may not encounter otherwise.

A comparative study of free-ranging rhesus macaques on Cayo Santiago, Puerto Rico demonstrated that the macaques form despotic groups as predicted by the phylogenetic model; but the degree to which they engaged in within-group competition varied by ecological factors such as group size and between-group competition (Balasubramaniam et al., 2014). The Cayo Santiago macaques have artificially-induced agonism through the introduction of high-quality, defensible feeding sites and thus differ from the Dead River macaques because the Cayo Santiago population is provisioned year-round with high-quality feeding and drinking stations while the Dead River group remain unprovisioned.

The Dead River macaques are unhabituated and unprovisioned, instead feeding on various food-types dispersed throughout the riverine floodplain (Riley and Wade, 2016). The study group also experiences little or no between-group competition due to the distance between the focal group and surrounding groups. Without the confounding factors from the Cayo Santiago study, the study group will be able to engage in undirected feeding practices which will result in a more accurate account of the typical group's strategy in their particular ecological context.

Given the study group's access to dispersed, comparable feeding sites (Monk, 1966; Riley and Wade, 2016), a lack of provisioning and human contact, and little to no between group competition, I predicted that the macaques would distribute across feeding sites within the floodplain and experience a shallow, tolerant hierarchy and infrequent agonistic interactions within a feeding context. This confirms predictions made by *EMFSR* and demonstrates that, while rhesus macaques generally conform to the typical despotic pattern, they also possess a high level of behavioral plasticity and adaptability, thus facilitating the exploitation of diverse habitats and available food-types.

It is important to acknowledge that rhesus macaques are a highly successful species that are dispersed throughout various habitats and often live commensally with humans (Richard et al., 1989), yet they are often the archetypal species for phylogenetic inertia (Thierry et al., 2000; Thierry, 2007; Balasubramaniam et al., 2012). Due to their success in various ecological conditions, rhesus macaques are not under dire threat from anthropogenic interference. As the archetype of phylogenetic inertia, any counterexample would call into question the efficacy of phylogenetic inertia in primate species and require a reconsideration of how rhesus macaque integrate into their ecosystem. Behavioral data were collected during summer in Florida when food is abundant so observations may not be indicative of year-round strategies. However, understanding the nature of phylogenetic inertia and its ability to constrain behavior is essential to addressing the anthropogenic pressure placed on other species that experience phylogenetic inertia but are also at risk from human encroachment and anthropogenic climate change (Strier, 2017).

CHAPTER 2: BACKGROUND

2.1: MODELS

Ecological models of female social relationships (*EMFSR*) have been used to explain social behavior between females in various taxa including antelope, bats, and birds (Jarman, 1974; Bradbury and Vehrencamp, 1977; Emlen, 1978). *EMFSR*, when applied to primates, attempts to resolve the relationship of social and ecological conditions with the observed agonistic behaviors (Isbell and Young, 2002). Three generations of ecological models attempt to explain the nature of female social relationships among primates by privileging various ecological factors as contributing to the observed behavioral patterns. These ecological factors are the proximate mechanisms for variations in social behavior and, given enough time, individual behavioral patterns will be selected for thus producing certain types of grouping patterns (Koenig, 2002).

The earliest attempt at creating a comprehensive ecological model to explain grouping patterns for primates was by Wrangham (1980), which used an ecological framework to explain the evolution of two types of female social organizations, referred to as *female-bonded* and *non-female-bonded*. This model suggests that when high quality foods are clumped, females would be philopatric, have stable dominance hierarchies, and engage in frequent intergroup aggression, thus being female-bonded. When high quality foods are distributed and indefensible, there would be female transfer, weak intra- and intergroup aggression, and weak or absent dominance hierarchies. Neo-tropical, ripe fruit specialists (Klein, 1974) confirmed the two-syndrome model; trees with high quality food are able to be defended and when conflict broke out, some individuals fled to neighboring trees. The winners of the dyadic interactions were able to monopolize these high food sources, thus resulting in the production of dominance hierarchies.

The strict dichotomy of the model, *female-bonded* and *non-female-bonded*, came under scrutiny when counterexamples were provided; patas monkeys (*Erythrocebus patas*) and blue monkeys (*Cercopithecus mitis*) exhibit female philopatry but lack stable dominance hierarchies. The same two species have also been documented to engage in frequent intergroup aggression but lack the stable dominance hierarchies predicted by Wrangham's model (Isbell and Young, 2002). Other species, like gelada baboons (*Theropithecus gelada*), forgo ripe fruit altogether that is available in the forests that border the grasslands where they feed (Dunbar and Dunbar, 1977). In order to accommodate the greater observed diversity of social patterns across various primate species, subsequent models separate within-group and between-group competition, and scramble competition (Jansen and van Schaik, 1988; Isbell, 1991; Sterck et al., 1997).

Further expanding upon the first generation, two-type model of Wrangham, van Schaik (1989) and Sterck et al. (1997) break primate social organization into four types that generally correspond with one another (Isbell and Young, 2002). *Dispersal-egalitarian* (Sterck et al., 1997) corresponds broadly to Wrangham's *non-female-bonded* classification. Groups that meet this classification have weak or unstable dominance hierarchies, female transfer (Sterck et al., 1997) or variable female transfer/philopatry (van Schaik 1989), high predation, and a lack of female coalitions (Sterck et al., 1997). *Resident-nepotistic* groups (Sterck et al., 1997) corresponds to Wrangham's *female-bonded* classification. These groups have highly expressed dominance hierarchies, coalitions, inheritance of maternal rank, female philopatry, formal signals of submission (Sterck et al., 1997), high predation, and grooming bonds (van Schaik, 1989). *Resident-egalitarian* groups (Sterck et al., 1997) exhibit female philopatry, strong between-group competition (van Schaik, 1989), weak within-group competition (Sterck et al. 1997), weak dominance hierarchies, intermediate to high predation, and female grooming bonds (van Schaik 1989). *Type D* (van Schaik, 1989) and *resident-nepotistic-tolerant* (Sterck et al., 1997) correspond loosely, describing groups that engage in female philopatry, inheritance of maternal rank, low predation, but differ on dominance hierarchies. *Resident-nepotistic-tolerant* predicts a highly expressed, stable dominance hierarchy whereas *Type D* predicts weak dominance hierarchies. The difference in the predicted strength of hierarchy is an important distinction given the social implication it has on the groups.

Comparative studies have demonstrated that variation exists within primate genera that inhabit different environments. In one such study (Barton et al., 1996), two species of savannah baboons (*Papio anubis* and *Papio ursinus*) exhibited different grouping strategies. Populations that inhabited areas with clumped food resources formed stable dominance hierarchies and had female philopatry, while the other had access to widely distributed food which dispersed the females and resulted in a loose hierarchy with female transfer. Predator density also correlated to time spent feeding at clumped sites. Populations at higher predation risk fed in more dense groups, engaged in more female-female grooming, and engaged in a higher supplant rate thus resulting in a stronger relationship between rank and food intake. These results conform to the model predictions. Groups that feed at high quality clumps with high predation risk aligned with

Type B/resident-nepotistic and groups that were able to disperse over multiple sites with low predation risk formed *Type A/dispersed-egalitarian* behavior.

The third-generation model (Isbell, 1991; Isbell and van Vuren, 1996; Isbell and Pruetz, 1998) forgoes the four-outcome model of van Schaik (1989) and Sterck et al. (1997) for a more concise three-syndrome model. The third-generation model privileges food abundance, food-site depletion time (*FSDT*), and within and between-group competition as the primary factors that determine social organization. The factors that take primacy in the second-generation models take secondary or tertiary roles in the Isbell and colleagues iteration. The distribution pattern of food, patchiness versus dispersed, is secondary to the abundance of food at a given site. In cases of clumped food resources (Balasubramaniam et al., 2014) food patchiness is difficult to measure but the monopolization of food and its usurpability is a measurable consequence of clumped food resources (Isbell and Young, 2002). Usurpability, the ability for a food resource to be taken from a lower ranking individual, makes these food sources contestable but is constrained by food-site depletion time. Sites with a short *FSDT* cannot be contested because they are exhausted before the individual can be usurped by a higher-ranking individual.

A food's monopolizability refers to the area in which a food source can be effectively controlled by a higher-ranking individual (Isbell and Young, 2002). There is an inverse relationship between the monopolizability of a food source and its distance from the individual (Mathy and Isbell, 2001). As the food source gets farther away from the individual, it becomes increasingly difficult for it to be controlled. Lower ranking individuals are less likely to obtain food in close proximity to a higher-ranking individual

(Schaub 1995) and as food sources become more spatially disassociated, higher ranking individuals cannot exclude others from all food sources (Mathy and Isbell, 2001).

Monopolizability and usurpability of food sources implies a dominance hierarchy. The three models all rely on dichotomous dominance hierarchies, strong (*female-bonded/resident-nepotistic*), in which rank is stable and reinforced through agonism juxtaposed to weak (*non-female-bonded/dispersal-egalitarian*), where rank is flexible or nonexistent. Although expressed in contrasting absolutes, the two types fall on a continuum with varying degrees of expression. The rate of expression can be determined by reversals that occur, violations of the generally observed dominance hierarchy (Isbell and Young, 2002). For groups that exhibit strong dominance hierarchies such as macaques, reversals occur in less than five percent of social interactions (Missakian, 1972; Isbell and Pruetz, 1998). Stability of the dominance hierarchy refers to the rate at which the dominance matrix, a statistical tool used to determine winners and losers of agonistic interactions, remains the same across two or more observed periods of time with complete stability when there is no deviation from the typical dominance hierarchy.

Groups of the first type, *contest and scramble competition for food both within and between groups,* exhibit a highly expressed, stable dominance hierarchy, maternal inheritance of rank, coalitions, and female philopatry. These groups experience high levels of competition between members of the same group as well as competition from surrounding social groups (Isbell, 1991). Food is limited and clumped, and therefore defensible. Groups that meet the second syndrome, *contest and scramble competition for food between groups; little or no contest or scramble food competition within groups*, exhibit weakly expressed or unstable dominance hierarchies, female philopatry, and a lack or absence of inheritance of maternal rank.

Groups that correspond to the second syndrome, c*ontest and scramble competition for food between groups; little or no contest or scramble food competition within groups*, exhibit weakly expressed or unstable dominance hierarchies, female philopatry, and a lack or absence of inheritance of maternal rank. Groups of this type are in competition with neighboring groups for high quality feeding sites but do not engage in frequent intragroup agonism (Isbell, 1991).

The final syndrome, *little or no contest or scramble competition of food within or between groups*, exhibits weak dominance hierarchies and female transfer. Groups of this type are able to distribute across multiple feeding sites and experience infrequent intragroup agonism and do not compete with other groups over food resources (Isbell, 1991).

The three generations of models agree that ecological pressures are the primary factor in primate social behavior. Primary ecological factors discussed in the literature include food distribution (Wrangham, 1980; van Schaik and van Hooff, 1983; van Schaik, 1989; Isbell, 1991), predation (van Schaik and van Hooff, 1983; van Schaik, 1989), population density (van Schaik and van Hooff, 1983; van Schaik, 1989), food abundance and food-site depletion time (Isbell, 1991; Isbell and van Vuren, 1996; Isbell and Pruetz, 1998). The similarities between the models are important but the differences are paramount to producing the most accurate model to describe and predict behavior.

A review of 20 species of primates (Isbell, 1991) evaluated the effects of ecological conditions on inter- and intragroup agonism. Females across various taxa group together which is paradoxical because it creates conspecific feeding competition and thus influences reproductive success. For groups that engage in high levels of intergroup competition, food abundance is an important factor in determining the level of intragroup competition. However, for groups that experience little between-group competition, the distribution of food is a more important factor than food abundance. A controlled experiment with captive rhesus macaques that tested the effects of food distance, abundance, and size in relation to agonistic behavior found that there was no significant difference between levels of agonism associated with food distance (Chancellor and Isbell, 2008). Agonism increased with larger food sites and higher food-site depletion times.

The ecological model of female social relationships has been criticized for being overly rigid while relying on a synthetic view of primate grouping and mating patterns that can be applied broadly across primate genera (Thierry, 2008). This assumes that different primate taxa will respond to the same ecological conditions in the same ways despite differences in evolutionary history and thus skillsets. Thierry discusses counter-instances in which the model fails to make accurate predictions. Lemurs fail to fit neatly into one of the four syndromes (Thierry, 2008) and female colobines disperse but possibly in order to find a male that defends the highest quality or largest resource (Fashing, 2001). Altering the model by expanding the variables in order to improve the predictive power will “inflate the model complexity” (Thierry, 2008: 95) thus resulting in too many combinations making the model untestable. Counterevidence to the model should not be met with additional hypotheses for the sake of confirming the predictions.

Based on the shortcomings proposed by Thierry, any socioecological model will fail resulting in better alternative explanations for social patterns among primates.

Koenig and Borries (2009) argue that, although the ecological model does have problems, the model should not be completely abandoned as suggested by Thierry (2008). There is a lack of comprehensive, inter-clade studies testing *EMFSR* in wild, unprovisioned taxa (Koenig et al., 2013). Koenig et al. (2013) also suggest that given the lack of a link between rates of agonism and hierarchical unidirectional consistency *between* clades but generally as predicted *within* clades and the role of phylogenetic relationships, researchers should recognize that *EMFSR* has limited utility and its potential use may be in examining variation within clades (2009).

Thierry (2007; 2008) and colleagues (2000) offer an alternative approach to understanding the cause of grouping patterns in some species and argue that there is an interplay between internal and external factors. Behavior cannot be reduced to ecological and sexual selection pressures as indicated by the ecological model. Behavior of the *Fascicularis* group (Richard et al., 1989) of macaques, which includes rhesus macaques, appears to have diverged from the suspected ancestral “type” as a part of the latest macaque radiation which coincides with human expansion and the aggressive temperament observed in rhesus macaques may be an adaptation or pre-adaptation to living commensally with humans (Thierry et al., 2000). Thus, rhesus macaques are an appropriate test case for *EMFSR*. Although individual behavior is quite adaptable, rhesus macaques exhibit a predictable pattern of social relationships (Thierry, 2007), where they engage in unidirectional agonism within a highly stable hierarchy across all studied locations.

Rhesus macaques live in multi-male multi-female groups with a female-biased sex ratio where offspring inherit the mother’s rank, with the youngest daughter holding the highest rank of her siblings resulting in a female-bonded grouping pattern. In a controlled experiment (Thierry, 2007), eight rhesus macaques were taken from their mothers to control for socially learned temperament and social style and hand-reared in a nursery. They were then slowly introduced to others in the experimental group. In the thirty years since the experiment began, the group has grown to over 100 individuals and exhibits the typical rhesus macaque grouping pattern including a despotic hierarchy. Without normal socialization and rearing, the test group still conformed to the predicted form. This indicates that although both the physical and social environment that the macaques inhabit play important roles in forming individual behavior, grouping patterns and group behavior are limited by some other factor. Therefore, Thierry argues that rhesus macaques experience phylogenetic inertia, limitations created by past evolutionary adaptations, caused by evolutionary pressure associated with proximity to humans which have constrained rhesus macaque behavior in a way that prevents the development of alternative grouping behaviors and thus undermines the effects of ecological pressures such as food distribution on forming macaque behavior.

2.2 STUDY SPECIES

Rhesus macaques (*Macaca mulatta*) are members of the *Fascicularis* group of macaques (Richard et al., 1989) which includes longtailed (*M. fascicularis*) and Japanese (*M. fuscata*) macaques, and are endemic to Central, Southern, and Southeast Asia; ranging from eastern Afghanistan through China, including some shallow water islands in the Bay of Bengal and the South China Sea (Fooden, 2000). The northern and western limits of their range are established by climatological and geographical factors, and the southern range is defined, loosely, by interspecific competition (Fooden, 2000; Kumar and Radhakrishna, 2011). Rhesus macaques inhabit a wide range of habitats, including temperate and subalpine forests, arid regions in western India and eastern Afghanistan, and needleleaf, mixed, but primarily broadleaf forests (Fooden, 1982; Goldstein and Richard 1989; Richard et al., 1989; Fooden, 2000; Lu et al., 2007).

Rhesus macaques live in multi-male multi-female groups of an average of 21.2 individuals (Fooden, 2000) although provisioned groups, like the introduced population on Cayo Santiago, Puerto Rico can be much larger, up to 264 (Balasubramaniam et al., 2014). Females are philopatric (resident) and generally exhibit a strict social hierarchy (despotic) enforced through varied levels of agonism (van Schaik, 1989; Sterck et al., 1997). Females inherit rank from their mothers, dominant to all individuals subordinate to her mother, subordinate to her mother, and the youngest daughter ranking highest among her sisters (Missakian, 1972), although Kutsukake (2000) demonstrated that this strict view of maternal inheritance does not hold up universally for all mother-daughter dyads.

Wild populations of rhesus macaques are omnivorous, primarily exploiting various plant types including flowers, fruits, grasses, and fungi but also relying on invertebrates (Fooden, 2000) and birds’ eggs (Anderson et al., 2016). Feeding often occurs in contested patches where dominant females have access to the highest quality clumps. The frequency of agonism is greater at these high-quality food patches (Balasubramaniam et al., 2014). However, most rhesus macaque groups do not live in undisturbed areas and often live commensally with humans, exploiting agriculture (Fooden, 2000; Thierry, 2007) and raiding urban areas such as markets and homes

(Saraswat et al., 2015). Richard et al. (1989) classifies rhesus macaques as the ecological category, “weed species”, because they often depend on and compete with humans throughout their native range; humans serve as competitor, predator, and host to rhesus macaque populations, which do well in anthropogenic spaces.

2.3 STUDY SITE

The study took place along the Ocklawaha and Dead Rivers, Florida, mostly in the Ocala National Forest. The river forms the western and northern borders of Ocala National Forest, from its southern point at Eureka Dam to Rodman Dam in the northeast. The floodplain of the river ranges from 0.8 to 1.6 km in width (Harms et al., 1980) and serves as an abundant food source for the macaques (Riley and Wade, 2016). The dominant plant community is a mixed deciduous hardwood forest, made up primarily of Carolina ash (*Fraxinus caroliniana*), bald cypress (*Taxodium distichum*), red maple (*Acer rubrum*), swamp tupelo (*Nyssa sylvatica*), cabbage palm (*Sabal palmetto*), and buttonbush (*Caphalantus occidentalis*) (Monk, 1966). These species form much of the diet of the macaques inhabiting central Florida (Wade and Riley, 2016).

The river and floodplain supports a diverse population of mammals including an introduced rhesus macaque (*M. mulatta*) population along the Silver, Ocklawaha, and Dead Rivers, white-tailed deer (*Odocoileus virginianus*), wild hogs (*Sus scrofa*), Northern river otters (*Lontra canadensis*), American black bear (*Ursus americanus*), and recent sightings of manatee (*Trichechus manatus*). The macaque population is also under predation pressure from bobcats (*Lynx rufus*) and American alligators (*Alligator mississippiensis*). Bobcats have been documented preying on introduced macaques in Texas (Gouzoules et al., 1975) and are likely a potential predator at this site as well.

There were two large alligators (~7ft and 9ft) that occupied the Dead River, near its confluence with the Ocklawaha River, where the macaques spent the majority of their feeding time during the duration of the study.

2.4 STUDY GROUP

In the mid-1930s, approximately six rhesus macaques were released on a small island in the Silver River in order to increase riverboat tourism (Wolfe and Peters, 1987; Anderson et al., 2017). However, rhesus macaques are strong swimmers and the island is not very isolated from the river banks. As such, the introduced macaques rapidly escaped and ultimately established a considerable breeding population along the Silver and Ocklawaha Rivers with unknown numbers that extend into Ocala National Forest. The initial introduction was bolstered by an additional six animals released in 1948. In total, the population reached ~400 animals in the 1980s (Wolfe and Peters, 1987). Current population estimates are only available for the Silver Springs State Park population along the Silver River. A 2013 study found 118 individuals in four groups (Riley and Wade, 2016); while current estimates stand at 190 individuals in five groups as of Spring 2016 (Anderson personal communication). However, no such estimates are currently available for the number of macaques that migrated from the Silver River and that have established an unknown number of groups along the Ocklawaha River (Anderson et al., 2017).

The Dead River macaque group is composed of 22 individuals: 12 females, 3 males, and 7 subadults and ranges along the Ocklawaha and Dead Rivers, north of Gores Landing (Fig. 5). The group primarily feeds in the floodplain of the rivers (Fig. 6). The study group is not habituated to humans, as they move away from the river when approached and thus there were no observed instances of provisioning by boaters. The Ocklawaha River is frequented by boats, both motorized and paddled, but the Dead River is much harder to navigate due to the dense vegetation, fallen trees, and confusing delta system near the confluence with the Ocklawaha River within the Ocala National Forest. When along the Dead River, the macaques are fairly isolated from human activity.

A study of the Silver River population of macaques found that, due to the lack of fruit available, the macaques were primarily exploiting leaves and other plant materials including moss and sedges (Riley and Wade, 2016). Ash trees formed the majority of their diet, 66.5%, with leaves, samaras, barks, flowers, and buds being consumed and the same types of trees are available along the Ocklawaha and Dead Rivers.

The study population differs from the parent population along the Silver River due to lack of provisioning and habituation. Riley and Wade (2016) found that 12.5% of the Silver River macaques' diet consisted of provisioned foods from kayakers. The macaques were also significantly more likely to ignore kayakers and canoers than motorized watercraft. The study population would move away from the river when approached within 10-15m. Whereas the Silver River population lives with and relies on humans for food, the Dead River macaque group was observed to actively avoid humans.

CHAPTER 3: METHODS

This project adheres to all ethical guideline of the university and was approved by University of North Carolina at Charlotte IACUC and US Forest Service.

3.1 Data Collection

I collected data in three phases. Observations during each phase were performed from a kayak using binoculars from >10m away. Each observation day began at 0800 and observations ended at 1700 if the study group remained within view of the river. The group's location was determined using a Garmin eTrex 20x and recorded in the research log. The feeding location from each observation day was inputted into Google Earth using degrees-minutes-seconds.

The first phase of the project was a pilot study, performed from March 25-27, 2016. The study feasibility, focal group's activity area, and composition were determined. The second phase took place from June 2-8, 2016. This phase was dedicated to the identification of the study subjects, including age-group and sex determination, recording identifying features for each individual, and an initial habituation period. The Dead River macaques are not habituated to humans and in order to avoid overexposure, an appropriate observation distance was determined, >10m (Johnson pilot study, 2016). I divided age-groups into three categories, *adult male, adult female,* or *subadult,* with each individual assigned a number to be used in a random number table to mitigate observer bias. Age-group is determined by an estimation of body weight; rhesus macaques become sexually mature with a minimum body weight of around 4kg (Fooden, 2000).

The final phase included behavioral observations from June 9-July 29. Data were collected using 1) focal animal sampling and 2) ad libitum notes. Focal animals were chosen using a random number table and individuals that were out of view were skipped and the next study subject in the table was selected. Agonistic interactions between adult females in the study group were recorded on the data collection sheet, noting interactions that occurred within a feeding context, winner and loser of each dyadic interaction, time, duration, and the assigned behavior code from the ethogram (Fig. 7) of expected behaviors (Balasubramaniam et al., 2014).

3.2 Data Analysis

Dyadic interactions were placed in a dominance matrix, indicating the number of agonistic interactions within a feeding context that each dyad experienced over the course of the study (June 2, 2016-July 29, 2016). Behaviors were grouped in two separate categories, contact (biting, hitting, attacking) and noncontact (displacement, threats/stares, avoidance). Although Cooper and Bernstein (2008) argue that contact aggression may not be a good predictor of dominance, I included these behaviors in order to evaluate whether there are differing strategies between high-ranking and low-ranking individuals when it comes to dominance interactions in a feeding context.

Hierarchy steepness was determined using David's score (*DS*) (David, 1988; Gammell et al., 2003), a standard method for establishing rank. *DS* compares the strengths within each dyadic interaction and corrects for chance wins (de Vries, 1998; de Vries et al., 2006). Individuals that often win dominance interactions have positive scores while subordinate individuals have negative scores. *DS* was determined in the statistical software Rstudio, using a package developed by Neumann et al. (2011). Scores were normalized (normDS) per de Vries et al. (2006) in order to run a typical least-squares linear regression to determine the steepness value (D_{ij}). Animals are ordered from the highest ranking (1) to the lowest ranking (11) on the *X* axis and normDS values are on the *Y* axis. Steepness varies between 0 and 1 when using normDS. Perfectly linear hierarchies have a slope of -1.0 thus having a steepness value of 1 (de Vries et al., 2006). The linear regression was completed in the statistical software, SPSS. Using Rstudio, I calculated the null hypothesis, the dominance index corrected for chance, as proposed by de Vries et al. (2006) by taking into account the binomial distribution with each individual having an equal chance of winning or losing each interaction. The correction is recommended when there are large differences in the numbers of interactions between the various dyads. Using D_{ij}, I ran a T-test to determine if there was a significant difference between it and the observed dyadic proportions of wins (P_{ij}) to the proportions corrected for chance (D_{ij}).

Stability was determined using Elo-rating (Albers and de Vries, 2001; Neumann et al., 2011). All individuals begin with the same arbitrary Elo-rating (1000) and their scores increase or decrease with each dyadic interaction, which is multiplied by a constant (k=100). Expected outcomes have smaller impacts on the change in Elo-ratings than do reversals. Elo-ratings provide a graphical representation of changes in hierarchy which allows for the monitoring of dominance relationships over time (Neumann et al., 2011). I determined Elo-ratings in Rstudio using a package developed by Neumann et al. (2011). Elo-ratings have been demonstrated to highly correlate to *DS* ranks (Albers and de Vries, 2001; Neumann et al., 2011) which allows them to be used together to understand group hierarchies.

From the Elo-ratings, I generated a win probability matrix (Fig. 4) in Rstudio using the Neumann et al. (2011) package. This matrix includes the probability that each individual will win a dyadic interaction. Using the Elo-rating data and win probabilities, I ran a 10,000-iteration simulation, in which randomly generated sequences of interactions were simulated and an average Elo-rating was given. The simulated Elo-Rating was then compared to the observed Elo-rating using a pair-sample t-test in SPSS.

Neumann et al. (2011) also proposes a method for determining a hierarchical stability index (*S*) over a given period of time. This index is approximate as it assumes that linear extrapolation of Elo-ratings including days in which not all individuals are present is appropriate. *S* is also weighted where rank reversals among high ranking individuals has a greater impact than reversals among the lowest ranking individuals. This assumes that rank reversals that occur in the highest-ranking individuals have more effect on hierarchy stability than does the lowest ranking (Neumann et al., 2011). *S* is limited to a range 0-1, with 1 indicating a perfectly stable hierarchy (Neumann and Kulik, 2014). *S* was determined for the entire study period as well as each month.

In order to analyze the relationship between rank and agonistic behaviors, I ran Spearman’s rho correlation (Loudon et al., 2005; Schülke et al., 2010). The correlation was determined for overall agonistic behaviors, as well as contact and noncontact interactions. Spearman’s rho is used to determine the relationship of two variables. Values fall between -1.0 and 1.0, with -1.0 being a perfect negative correlation and 1.0 a perfect positive correlation.

CHAPTER 4: RESULTS

During the study period, the group was located on 84.4% of sampling effort days (N = 38/45) with a mean of 6.1 hours observed per day between June 3-July 29, 2016. The study group feeds along the both the Ocklawaha and Dead Rivers but was observed to utilize the Dead River at a higher frequency (81.6%, N = 31) (Fig. 6).

During the study, 88 incidents of agonistic behavior over 38 days and 231.5 hours were observed with a frequency of 0.35 agonistic interactions per hour. The average time observed per individual is 21.05 hours with a minimum of 18 hours (DRe) and maximum of 25.5 (DRf). 11 of the 12 females in the group were observed to engage in agonistic behavior with the two highest ranking females, DRa (20 interactions) and DRf (17 interactions), having the most agonistic interactions (Table 3; Fig. 2). The three highest ranking females engaged in agonistic behavior most frequently (DRa = 0.85/hr; DRf = 0.67/hr; DRb = 0.60/hr). Mid-ranking individuals engaged in agonistic behavior least frequently (DRk = 0.05/hr; DRi = 0.10/hr; DRl = 0.28/hr; DRg = 0.13/hr) and the lowest ranking intermediary (DRc = 0.49/hr; DRd = 0.32/hr).

Using the normalized David's Score (normDS) (de Vries et al., 2006), I calculated the observed steepness of the hierarchy (Table 1; Fig. 3) using a least-squares linear regression to find the best-fitting straight line (F (1,9) = 220.258, p = <0.05) with a slope of Y= -0.301x + 6.808 therefore, the steepness value is P_{ij}=0.301 (de Vries et al., 2006). The steepness of the corrected normDS (F (1,9) = 115.804, p= <0.05) is D_{ij}=0.198. There is a significant difference in the steepness of the slopes between P_{ij} and D_{ij} (T (18) = 3.82796, p = 0.00123).

Using Elo-ratings stability index (*S*), outlined by Neumann et al. (2011), the study group has a stability index of 0.9747, with 1.0 being a perfectly stable hierarchy. Using Elo-rating, changes in hierarchy were tracked over the duration of the study (Table 4). Mean Elo-ratings for each individual range from the highest rated individual at 1250.75 (DRa) to the lowest ranking at 866.269 (DRd) (Table 1). A visual representation of Elo-ratings (Fig. 1) demonstrates that there are frequent reversals within the mid and low-ranking individuals. Elo-rating predicts a different hierarchy than David's Score. The top two ranked individuals remain the same but both the final and Mean Elo-ratings predict different rankings for all but one (DRe) of the lower ranking individuals.

Examining the relationship between rank and overall agonistic behaviors, I found that there is a positive correlation between rank and agonism (r_s= 0.473, p=0.142). Further examination between types of agonism (contact and non-contact) demonstrate that there is a difference in strategy between rank and the type of agonistic behavior. There is a negative correlation between rank and contact aggression (r_s=-0.524, p=0.098) and a positive correlation between rank and non-contact agonism (r_s= 0.527, p=0.096).

CHAPTER 5: DISCUSSION

The Dead River macaque group, located 12km north of the parent population on the Silver River, were previously unstudied. The goal of this project was to examine the effect of a novel environment on the expression of female hierarchy by focusing on agonistic interactions within a feeding context. There are conflicting expectations for how the group will organize given the two standard approaches to understanding rhesus macaque social hierarchy. On one hand, the ecological model predicts that the environment plays a central role in determining behavior and social organization (van Schaik, 1989; Isbell, 1991; Sterck et al., 1997; Isbell and Pruetz, 1998; Isbell and Young, 2002), while the phylogenetic model (Thierry et al., 2000; Thierry, 2007) predicts conformity to the archetypal rhesus macaque social schema due to phylogenetic inertia.

The study confirms observations from Gottschalk (2011), and Riley and Wade (2016) that the central Florida macaque population is primarily feeding in the floodplain. The Dead River macaques were located on 84.4% of sampling effort days (N = 38/45). The group was more likely to not be found during periods of time where kayak and canoe tours occurred more frequently. As the summer progressed and the number of people on the river increased, the macaques moved from the Ocklawaha River to the Dead River (Fig. 6).

The Dead River is less frequented by boaters due to dense vegetation which obscures access to the river and two large alligators (~9ft, ~7ft) near its confluence with the Ocklawaha River. The study group avoids human contact and this behavior is very different from that observed among the Silver River groups. Riley and Wade (2016) found that the macaques are exploiting boaters for food and 11.5% (N = 65/566) of boats engage in provisioning. During the study, the Dead River macaques were never observed to feed on provisioned food and would move away from the river if approached by boaters. A possible explanation for the different strategies is that the Dead River macaques are in an area that experiences less boat traffic and have space to retreat to if over-exposed to human activity.

The group frequently feeds within the Ocala National Forest, where the majority of observations occurred, and this area is fairly remote. During the study, there were no days in which people were observed while the study group was on the Dead River, whether on the river or in the national forest. In contrast, The Silver River macaques are constantly exposed to boaters because the river flows through Silver Springs State Park (SSSP). SSSP receives over 200,000 visitors annually (Florida Department of Environmental Protection, 2012) which increases the frequency at which the macaques are exposed to people, thus leading to a higher level of habituation. In controlled experiments, Clay et al. (2008) found that desensitization and habituation lower fear responses in rhesus macaques. Consistent exposure to human activity with provisioning included may have differentiated behavior between the macaques on the Silver River and those along the less frequented Ocklawaha and Dead Rivers. The effects of close human contact through tourism and provisioning have been shown to change behavior across various species of macaques throughout Gibraltar, North Africa, and Asia (Fuentes, 2010; Fuentes et al., 2007; O’Leary and Fa, 1993).

Over 231.5 hours of observation time, there were 88 instances of agonism within feeding context among focal animals, with a frequency of 0.35 agonistic interactions per hour. The distribution of agonism, high-ranking with the highest frequency (Fig. 2), conforms to the expected pattern seen in rhesus macaques and other closely related species (Chapais, 1988; Yamagiwa and Hill, 1998; Thierry, 2007). Higher frequencies of directional agonism seen among the highest-ranking individuals in social groups serve to maintain status and increase access to food resources (Isbell, 1991; van Schaik and Hrdy, 1991; Bercovitch and Strum, 1993; Sterck et al., 1997; Koenig et al., 1998). Takahata et al. (1998; 1999) and Gouzoules et al. (1982) have demonstrated that there is not a significant difference in reproductive fitness between high-ranking females and low-ranking females in *Macaca fuscata.* However, this has been contradicted in other groups of primates such as chimpanzees (Pusey et al., 1997), baboons (Samuels et al., 1987; Silk et al., 2003) and langurs (Borries et al., 1991) where there was a strong correlation between rank and reproductive success, including infant survival; juvenile survival was more variable across taxa. In a study by van Noordwijk and van Schaik (1999), rank was an important factor in reproductive success and infant survival among *Macaca fascicularis,* primarily in large groups due to a greater chance for maternal survival during peak reproductive age but was less significant in small and medium size groups. Given the variability of findings across primate taxa, it is difficult to determine the effect of rank on reproductive success in the study group. The close phylogenetic relationship to both *M. fascicularis* and *M. fuscata,* and the group size indicates that there may be little reproductive success associated with rank in the study group. The lack of reproductive benefit may explain the lack of observed steepness of rank in the Dead River macaques.

Analyzing the relationship between the steepness of observed normDS (P_{ij}) and corrected *DS* (D_{ij}), there is a significant difference in the slopes. The steepness value of the P_{ij} (0.301) is much higher than the null hypothesis, D_{ij} (0.198). This indicates that the difference in the numbers of interactions (i.e. DRa = 20, DRk = 1) between the various dyads may artificially inflate the steepness value (de Vries et al., 2006). When corrected using D_{ij}, the hierarchy becomes more shallow which is indicative of the number of reversals throughout the study, particularly among the lower ranking individuals. Although the observed steepness value is higher than the null hypothesis, both still indicate a relatively shallow hierarchy (Fig. 3). As reported by Balasubramaniam et al. (2012), rhesus macaques in other studies had a P_{ij} of 0.80 and D_{ij} of 0.65 which is indicative of a very steep hierarchy. Greater variability in steepness was demonstrated among the closely related *M. fuscata* and *fascicularis* (Balasubramaniam et al., 2012), although each had much steeper hierarchies than the study group. The fairly shallow hierarchy observed in the study group violates expectations set by the phylogenetic model (Thierry et al., 2000; Thierry, 2007; 2008). The phylogenetic model predicts a steep hierarchy which cannot be violated without drastic change and new, strong selective pressures. However, toleration has been observed in rhesus macaques within feeding context, albeit in consortship dyads (Dubuc et al., 2012). Although rhesus macaques are generally highly despotic, under certain circumstances, they have been shown to be tolerant. The distribution of primary foods throughout the floodplain allows for the individuals in the study group to feed at separate, comparable feeding sites and so *FSDT* and size of sites do not have a significant impact on interactions; the macaques do not need to compete for high-quality feeding sites and also experience no observed between-group competition. This indicates that the macaques are adapting behavior to match ecological opportunities in the immediate environment and are not restricted to a behavioral pattern based on adaptation to a past environment.

Elo-rating stability index (*S*) indicates that the study group experiences a high level of stability ($S = 0.9747$). *S* privileges reversals at the top of the hierarchy over those at the bottom and so the stability index is inflated due to the infrequency of reversals among the highest-ranking females. This is based on the assumption that instability at the top of the hierarchy has a greater impact on social stability than instability among the lower ranking individuals (Neumann et al., 2011). The lowest ranking female, DRd, experienced the most reversals of any individual ($N = 6$). Four out of six reversals occurred between DRd and low-ranking individuals (DRc and DRe), one with a mid-ranking female (DRl), and one with a high-ranking female (DRh). The highest-ranking female (DRa) experienced one reversal, where she was chased away from a feeding site but retaliated after retreating by displacing the former. The asymmetrical nature of the reversals is further evidence for the differential strategies among rank groups in the Dead River macaques.

An evaluation of Elo-ratings throughout the duration of the study demonstrates that the hierarchy experiences variable stability across the rank groups (Fig. 1). The highest-ranking individuals experience a high level of stability with very few unexpected dyadic outcomes. Mid and low-ranking individuals undergo frequent reversals. This is in-line with findings by Kutsukake (2000) and Chapais (1985; 1988) for the closely related *M. fuscata*, where high-ranking females experience greater stability than do lower ranking females. Asymmetry in stability based on rank may be caused by 1) high-ranking females having more active allies than lower ranking (Chapais, 1992), and 2) lower ranking females attempting to create bridging alliances with high-ranking females at the expense of kin cohesion (Chapais, 1992). Although the second possible cause cannot be confirmed without genetic data to determine maternal relationships, there are observed alliances in this group between individuals that belong to different rank groups. One such relationship was observed in the DRf/DRg dyad of the study group. This dyad was always observed together and experienced the highest rate of agonism of any dyad. DRf held the second highest-ranking position in the hierarchy during the duration of the study while DRg was the second lowest ranking female according to Elo-rating. For nearly every instance in which DRg was the recipient of directional agonism, DRf would retaliate against the perpetrator. Again, analysis on group stability violates the expectations of the phylogenetic model (Thierry et al., 2000; Thierry, 2007; 2008).

The group is expected to demonstrate a stable, despotic hierarchy with few reversals as is typical among rhesus macaques, classified normally as *resident-nepotistic-despotic* or *Type B* (van Schaik, 1989; Sterck et al., 1997; Thierry, 2007). However, apart from the highest-ranking individuals (DRa, DRf), the group experiences frequent reversals and dispersed feeding as is observed among more tolerant groups (Fig. 1) (Sterck et al., 1997). The Dead River macaques appear to most closely conform to the *Type D* (van Schaik, 1989) grouping strategy, which includes a weak dominance hierarchy under low predation pressure. During the study, there were no observed instances of predation upon the group despite dispersal across multiple feeding sites; the number of individuals remained stable throughout. Groups under high predation risk tend to feed in clumped groups in order to lower each individual’s risk (van Schaik et al., 1983; van Schaik, 1989; van Schaik et al., 1996; Sterck et al., 1997), but this also creates greater opportunity for intragroup agonism (Barton et al., 1996). Thus, the study group appears to be modifying their behavior in response to ecological conditions, such as food availability, high *FSDT*, and a greater reliance on leaves and samaras of ash trees that make up the majority of their diet (Riley and Wade, 2016) and dominate the mixed swamp forests (Monk 1966) that the macaques are exploiting.

The study group experiences an asymmetrical distribution on agonism. While the highest-ranking individuals had the most agonistic interactions, the types of interactions differed by rank. The highest ranking individuals engaged in non-contact agonism most frequently, with the top-ranking individual (DRa) having no observed instances of contact agonism. However, the lowest ranking individuals engaged in contact agonism more often. Even with the differential distribution of agonistic types by rank, contact agonism occurred infrequently in general. Of 88 instances of agonism across 231.5 hours of observation, contact agonism was only observed five times, which makes up less than 6% of all observed agonistic interactions. In order for low-ranking individuals to dominate higher ranking individuals, they may have to engage in more contact agonism to win the interaction, whereas high ranking individuals are able to displace lower-ranking individuals without attack.

This study demonstrates that rhesus macaques are capable of adapting social behavior and grouping patterns to novel conditions. However, one limitation of the study is seasonality and time. The study took place over the summer when food was abundant and so the macaques were able to feed across dispersed sites. This limited the number of interactions in a feeding context and lessened opportunity for competition. During winter months when food is more limited, there could be increased competition and thus agonism. However, ash trees provide food year-round (Riley and Wade, 2016) and are abundant and may not represent a limiting factor. Seasonal difference in grouping strategies would further confirm rhesus macaques' ability to adapt to ecological conditions. The duration of the study also limited the results, taking place over 51 days, and was performed by one researcher. A longer study would serve to provide a larger sample of the group's behavior and the effects of river use, seasonality, and human contact across longer periods of time. Nevertheless, the observations of deviations from the species-typical pattern at any point of the year support my conclusion that macaques at this site are exhibiting a degree of behavioral flexibility not predicted by the phylogenetic model.

Future research should take place over multiple seasons in order to see how group behavior changes with food availability. Adding another researcher to the project would increase hours of observations, getting more samples per individual and increase inter-observer reliability. A challenge with adding more people to the site would increase the likelihood that the group becomes more habituated, which may have unintended consequences. This study focuses on individual behavior within particular ecological conditions but an evaluation of how the introduced population of macaques are integrated into and construct their ecological niche in central Florida may have greater implications, particularly for conservation and management, both at this site and at other macaque sites.

CHAPTER 6: CONCLUSION

Findings from this project conform to expectations set out by the ecological model for female social relationships (*EMFSR*) (van Schaik, 1989; Isbell, 1991; Sterck et al., 1997; Isbell and Pruetz, 1998) and fail to conform to the phylogenetic model proposed by Thierry and colleagues (2000; 2008). Given the distribution and abundance of food-sites throughout the floodplain, the macaques are able to disperse across several sites, thus limiting the number of agonistic interactions over food. Multiple statistical approaches to understanding the organization of the hierarchy of the study group indicate that there is potential for variability.

This study elicits a new question: if rhesus macaques can break from the typical *Macaca mulatta* grouping pattern, why is the *resident-nepotisitc-despotic* pattern so pervasive (Sterck et al., 1997; Thierry, 2007; 2008; Balasubramaniam et al., 2012)? This pattern is observed across rhesus macaque populations throughout their native range and across various habitats and so there must be something adaptive to despotic hierarchies. Furthermore, understanding a species that is the archetype for behavioral phylogenetic inertia may permit a greater understanding of how other taxa that are at risk of ecological upheaval through habitat loss, human encroachment, or anthropogenic climate change may adapt to rapidly changing and new ecological conditions. We have a broad understanding of many aspects of primate behavior and ecology but fail to understand how their behavior contributes to their resilience and ability to adapt to rapid environmental changes (Strier, 2017). Rhesus macaques are the most widespread primate species (Fooden, 2000), other than humans, and are successful in all habitats, either in native or introduced groups (Kumar and Radhakrishna, 2011; Balasubramaniam et al., 2014). We do not understand why some species and populations are more successful than others and a greater focus on intraspecific variation can provide conservation efforts with a greater pool of knowledge to draw from.

Individual and group behavior must be flexible to adapt to rapidly changing circumstances, both in regards to increased contact with humans and anthropogenically altered ecosystems as we continue to expand. Rhesus macaques have demonstrated their ability to adapt and live alongside humans successfully (Thierry et al., 2000). Results from studies like this may inform conservation efforts, which have become a priority among primate scientists as more species come under greater anthropogenic pressure (Strier, 2017). Species that are unable to track behaviorally with environmental changes are at a higher risk of extinction and these species will need special attention to protect them in the face of increasing anthropogenic pressure.

Beyond the broad implications of understanding the relationship between primate species and their environment, this study can serve an applied purpose. Given that the Florida macaques are an introduced population, more research should be performed in order to mitigate ecological issues that could arise. The effects that the macaques have on the local flora and fauna, such as predation of the eggs of endemic bird species (Anderson et al., 2016), disease transmission (Huff and Barry, 2003), and as reservoirs for vector-borne illnesses like zika (Dudley et al., 2016) are important considerations when evaluating management plans. There is also no information on the carrying capacity of the local environment and rhesus macaque competition with local taxa and thus the long-term effects of uncontrolled breeding among the groups across Florida.

REFERENCES

Albers PC, and de Vries H. 2001. Elo-rating as a tool in the sequential estimation of dominance strengths. Academic Press.

Anderson CJ, Hostetler ME, and Johnson SA. 2017. History and Status of Introduced Non-Human Primate Populations in Florida. Southeastern Naturalist 16(1):19-36.

Anderson CJ, Hostetler ME, Sieving KE, and Johnson SA. 2016. Predation of artificial nests by introduced rhesus macaques (*Macaca mulatta*) in Florida, USA. Biological Invasions 18(10):2783-2789.

Balasubramaniam K, Dittmar K, and Berman C. 2012. Hierarchical steepness and phylogenetic models: phylogenetic signals in *Macaca*. Animal Behavior 83:2007-2018.

Balasubramaniam K, Dunayer E, Gilhooly L, Rosenfield K, and Berman C. 2014. Group size, contest competition, and social structure in Cayo Santiago rhesus macaques. Behaviour 151(12-13):1759-1798.

Barton RA, Byrne RW, and Whiten A. 1996. Ecology, feeding competition and social structure in baboons. Behavioral Ecology and Sociobiology 38(5):321-329.

Bercovitch FB, and Strum SC. 1993. Dominance rank, resource availability, and reproductive maturation in female savanna baboons. Behavioral Ecology and Sociobiology 33(5):313-318.

Berman CM, and Kapsalis E. 2009. Variation over time in grooming kin bias among female rhesus macaques on Cayo Santiago supports the time constraints hypothesis. American Journal of Physical Anthropology 48(1):89-90.

Borries C, Sommer V, and Srivastava A. 1991. Dominance, age, and reproductive success in free-ranging female Hanuman langurs (*Presbytis entellus*). International Journal of Primatology 12(3):231-257.

Bradbury JW, and Vehrencamp SL. 1977. Social organisation and foraging in emballonurid bats. Behavioral Ecology and Sociobiology 36(1):1-17.

Demaria C, and Thierry B. 2001. A comparative study of reconciliation in rhesus and Tonkean macaques. Behaviour 138(1):397-410.

Chancellor RL, and Isbell LA. 2008. Punishment and competition over food in captive rhesus macaques, *Macaca mulatta*. Animal Behaviour 75(6):1939-1947.

Chapais B. 1985. An experimental analysis of a mother-daughter rank reversal in Japanese macaques (*Macaca fuscata*). Primates 26(4):407-423.

Chapais B. 1988. Rank maintenance in female Japanese macaques: experimental evidence for social dependency. Behaviour 104(1):41-58.

Chapais B. 1992. The role of alliances in social inheritance of rank among female primates. Coalitions and alliances in humans and other animals:29-60.

Charmantier A, McCleery RH, Cole LR, Perrins C, Kruuk LE, and Sheldon BC. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. Science 320(5877):800-803.

Clay AW, Bloomsmith MA, Marr MJ, and Maple TL. 2008. Habituation and desensitization as methods for reducing fearful behavior in singly housed rhesus macaques. American Journal of Primatology 71(1):30-39.

Cooper MA, and Bernstein IS. 2008. Evaluating dominance styles in Assamese and rhesus macaques. International Journal of Primatology 29(1):225-243.

David HA. 1963. The method of paired comparisons. 12. London.

Dubuc C, Hughes KD, Cascio J, and Santos LR. 2012. Social tolerance in a despotic primate: Co-feeding between consortship partners in rhesus macaques. American Journal of Physical Anthropology 148(1):73-80.

Dudley DM, Aliota MT, Mohr EL, Weiler AM, Lehrer-Brey G, Weisgrau KL, Mohns MS, Breitbach ME, Rasheed MN, and Newman CM. 2016. A rhesus macaque model of Asian-lineage Zika virus infection. Nature communications 7.

Dunbar RI, and Dunbar EP. 1977. Dominance and reproductive success among female gelada baboons. Nature 266(5600):351-352.

Emlen ST. 1978. The evolution of coopoerative breeding in birds. In: Krebs JR, and Davis NB, editors. Behavioural Ecology. Oxford: Blackwell Scientific Publishing. p 245-281.

Fashing PJ. 2001. Male and female strategies during intergroup encounters in guerezas (*Colobus guereza*): evidence for resource defense mediated through males and a comparison with other primates. Behavioral Ecology and Sociobiology 50:219-230.

Florida Department of Environmental Protection. 2012. Florida state parks annual attendance.

Fooden J. 1982. Ecogeographic Segregation of Macaque Species Primates 23(4):574-579.

Fooden J. 2000. Systematic review of the rhesus macaque, *Macaca mulatta* (Zimmermann, 1780). Fieldiana: Zoology 90:1-180.

Fuentes A. 2010. Naturalcultural encounters in Bali: Monkeys, temples, tourists, and ethnoprimatology. Cultural Anthropology 25(4):600-624.

Fuentes A, Shaw E, and Cortes J. 2007. Qualitative assessment of macaque tourist sites in Padangtegal, Bali, Indonesia, and the Upper Rock Nature Reserve, Gibraltar. International Jounal of Primatology 28(5):1143-1158.

Gammell MP, Vries Hd, Jennings DJ, Carlin CM, and Hayden TJ. 2003. David's score: a more appropriate dominance ranking method than Clutton-Brock et al.'s index. Animal Behaviour 66(3):601-605.

Goldstein SJ, and Richard AF. 1989. Ecology of rhesus macaques (*Macaca mulatta*) in Northwest Pakistan. International Journal of Primatology 10(6):532-567.

Gottschalk B. 2011. Study of the Silver River Monkeys. Report to Florida DEP/Bureau Parks, District 3.

Gouzoules H, Fedigan LM, and Fedigan L. 1975. Responses of a transplanted troop of Japanese macaques (*Macaca fuscata*) to bobcat (*Lynx rufus*) predation. Primates 16(3):335-349.

Gouzoules H, Gouzoules S, and Fedigan L. 1982. Behavioural dominance and reproductive success in female Japanese monkeys (*Macaca fuscata*). Animal Behaviour 30(4):1138-1150.

Harms WR, Schreuder HT, Hook DD, and Brown CL. 1980. The Effects of Flooding on the Swamp Forest in Lake Ocklawaha, Florida. ECY Ecology 61(6):1412-1421.

Hoeck HN, Klein H, and Hoeck P. 1982. Flexible Social Organization in Hyrax. Ethology 59(4):265-298.

Huff JL, and Barry PA. 2003. B-virus (Cercopithecine herpesvirus 1) infection in humans and macaques: potential for zoonotic disease. Emerging Infectious Diseases 9(2):246-250.

Isbell LA. 1991. Contest and scramble competition: patterns of female aggression and ranging behavior among primates. Behavioral Ecology 2(2):143-155.

Isbell LA, and Pruetz JD. 1998. Differences Between Vervets (*Cercopithecus aethiops*) and Patas Monkeys (*Erythrocebus patas*) in Agonistic Interactions Between Adult Females. International Journal of Primatology 19(5):837-855.

Isbell LA, and Young TP. 2002. Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. Behaviour 139(2):177-202.

Janson CH, and van Schaik CP. 1988. Recognizing the many faces of primate food competition: methods. Behaviour 105(1):165-186.

Jarman PJ. 1974. The social organization of antelope in relation to their ecology. Behaviour 48(1):215-267.

Klein LL. 1974. Agonistic behavior in neotropical primates. Academic Press, New York. p 77-122.

Koenig A. 2002. Competition for Resources and Its Behavioral Consequences Among Female Primates. International Journal of Primatology 23(4):759-783.

Koenig A, Beise J, Chalise MK, and Ganzhorn JU. 1998. When females should contest for food–testing hypotheses about resource density, distribution, size, and quality with Hanuman langurs (*Presbytis entellus*). Behavioral Ecology and Sociobiology 42(4):225-237.

Koenig A, and Borries C. 2009. The lost dream of ecological determinism: Time to say goodbye? Or a White Queen's proposal? Evolutionary Anthropology 18(5):166-174.

Koenig A, Scarry CJ, Wheeler BC, and Borries C. 2013. Variation in grouping patterns, mating systems and social structure: what socio-ecological models attempt to explain. Phil Trans Roy Soc Biol 368(1618).

Kumar R, and Radhakrishna S. 2011. Of Least Concern? Range Extension by Rhesus Macaques (*Macaca mulatta*) Threatens Long-Term Survival of Bonnet Macaques (*M. radiata*) in Peninsular India. International Journal of Primatology 32(4):945-959.

Kutsukake N. 2000. Matrilineal rank inheritance varies with absolute rank in Japanese macaques. Primates 41(3):321-335.

Loudon JE, Fuentes A, and Welch AR. 2005. Agonism and Affiliation: Adult Male Sexual Strategies Across One Mating Period in Three Groups of Long-Tailed Macaques (*Macaca fascicularis*). Laboratory Primate Newsletter:12.

Lu J, Hou J-H, Wang H-F, and Qu W-Y. 2007. Current Status of *Macaca mulatta* in Taihangshan Mountains Area, Jiyuan, Henan, China. International Joural of Primatology 28(5):1085-1091.

Lynne AI, and van Vuren D. 1996. Differential Costs of Locational and Social Dispersal and Their Consequences for Female Group-Living Primates. Behaviour 133(1/2):1-36.

Mathy JW, and Isbell LA. 2001. The Relative Importance of Size of Food and Interfood Distance in Eliciting Aggression in Captive Rhesus Macaques (*Macaca mulatta*). Folia Primatologica 72(5):268-277.

Missakian EA. 1972. Genealogical and cross-genealogical dominance relations in a group of free-ranging rhesus monkeys (*Macaca mulatta*) on Cayo Santiago. Primates 13(2):169-180.

Monk CD. 1966. An Ecological Study of Hardwood Swamps in North-Central Florida. Ecology 47(4):649-654.

Neumann C, Duboscq J, Dubuc C, Ginting A, Irwan AM, Engelhardt A, Widdig A, and Agil M. 2011. Assessing dominance hierarchies: Validation and advantages of progressive evaluation with Elo-rating. Animal Behaviour 82(4):911-921.

Neumann C, and Kulik L. 2014. EloRating: Animal dominance hierarchies by Elo rating. R package version 043:1-26.

van Noordwijk MA, and van Schaik CP. 1999. The effects of dominance rank and group size on female lifetime reproductive success in wild long-tailed macaques, *Macaca fascicularis*. Primates 40(1):105-130.

O'Leary H, and Fa JA. 1993. Effects of tourists on Barbary macaques at Gibraltar. Folia Primatologica 61(2):77-91.

Pusey A, Williams J, and Goodall J. 1997. The influence of dominance rank on the reproductive success of female chimpanzees. Science 277(5327):828-831.

Richard AF, Goldstein SJ, Dewar RE. 1989. Weed macaques: the evolutionary implications of macaque feeding ecology. International Journal of Primatology 10(6):569-594

Riley EP, and Wade TW. 2016. Adapting to Florida’s riverine woodlands: the population status and feeding ecology of the Silver River rhesus macaques and their interface with humans. Primates 57(2):1-16.

Samuels A, Silk JB, and Altmann J. 1987. Continuity and change in dominance relations among female baboons. Animal Behaviour 35(3):785-793.

Saraswat R, Sinha A, and Radhakrishna S. 2015. A god becomes a pest? Human-rhesus macaque interactions in Himachal Pradesh, northern India. European Journal of Wildlife Research 61(3):435-443.

van Schaik CP, and Van Hooff JARAM. 1983. On the Ultimate Causes of Primate Social Systems. Behaviour 85(1-2):91-117.

van Schaik CP, van Noordwijk MA, Warsono B, and Sutriono E. 1983. Party size and early detection of predators in sumatran forest primates. Primates 24(2):211-221.

van Schaik CP. 1989. The ecology of social relationships amongst female primates. In: Standen V, and Foley RA, editors. Comparative Socioecology. Oxford, UK: Blackwell Scientific. p 195-218.

van Schaik CP. and Hrdy SB. 1991. Intensity of local resource competition shapes the relationship between maternal rank and sex ratios at birth in cercopithecine primates. The American Naturalist 138(6):1555-1562.

van Schaik CP. van Amerongen A, and van Noordwijk MA. 1996. Riverine refuging by wild Sumatran long-tailed macaques (*Macaca fascicularis*). In: Fa JA, and D.G. L, editors. Evolution and ecology of macaque societies. Cambridge, UK: Cambridge University Press. p 160-181.

Schaub H. 1995. Dominance fades with distance: an experiment on food competition in long-tailed macaques (*Macaca fascicularis*). Journal of Comparative Psychology 109(2):196-202.

Schülke O, Bhagavatula J, Vigilant L, and Ostner J. 2010. Social bonds enhance reproductive success in male macaques. Current Biology 20(24):2207-2210.

Silk JB, Alberts SC, and Altmann J. 2003. Social bonds of female baboons enhance infant survival. Science 302(5648):1231-1234.

Smith JLD. 1993. The Role of Dispersal in Structuring the Chitwan Tiger Population. Behaviour 124(3):165-195.

Sterck EH, Watts DP, and van Schaik CP. 1997. The evolution of female social relationships in nonhuman primates. Behavioral Ecology and Sociobiology 41(5):291-309.

Strier KB. 2017. What does variation in primate behavior mean? American Journal of Physical Anthropology 162(S63):4-14.

Takahata Y, Suzuki S, Agetsuma N, Okayasu N, Sugiura H, Takahashi H, Yamagiwa J, Izawa K, Furuichi T, Hill DA, et al. 1998. Reproduction of wild Japanese macaque females of Yakushima and Kinkazan Islands: A preliminary report. Primates 39(3):339-349.

Thierry B, Singh M, Kaumanns W. 2004. Macaque societies: a model for the study of social organization. Vol 41. Cambridge University Press.

Thierry B. 2007. Unity in diversity: Lessons from macaque societies. Evolutionary Anthropology 16(6):224-238.

Thierry B. 2008. Primate socioecology, the lost dream of ecological determinism. Evolutionary Anthropology 17(2):93-96.

Thierry B, Iwaniuk AN, and Pellis SM. 2000. The Influence of Phylogeny on the Social Behaviour of Macaques (Primates: Cercopithecidae, genus *Macaca*). Ethology 106(8):713-728.

de Vries H. 1998. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. Animal Behaviour 55(4):827-843.

de Vries H, Stevens JM, and Vervaecke H. 2006. Measuring and testing the steepness of dominance hierarchies. Animal Behaviour 71(3):585-592.

Wolfe LD, and Peters EH. 1987. History of freeranging rhesus monkeys (*Macaca mulatta*) of Silver Springs. Florida Scientist 50(4):234-245.

Wrangham RW. 1980. An ecological model of female-bonded primate groups. Behaviour 75(3):262-300.

Yamagiwa J, and Hill DA. 1998. Intraspecific variation in the social organization of Japanese macaques: Past and present scope of field studies in natural habitats. Primates 39(3):257-273.

APPENDIX A: TABLES

Table 1: Hierarchy Ratings. This table includes David’s Scores, both the observed normDS(P_{ij}) and corrected DS(D_{ij}), and Elo-ratings. Mean Elo was calculated by taking the average Elo-rating over the course of the study. Final Elo refers to the final scores for each individual at the end of the study period. Simulated Elo was calculated in Rstudio by running a 10,000-iteration simulation of Elo-ratings by using calculated win probabilities (Table 2). The study subjects are ordered by rank determined by P_{ij}.

ID	**DS(P*ij*)**	**DS(D*ij*)**	**Mean Elo**	**Final Elo**	**Simulated Elo**
a	6.94697	6.415801	1250.8	1348.0	1158.9
f	5.848485	5.34848	1086.9	1194.0	1133.5
b	5.780303	5.514394	1022.5	1150.0	1013.1
h	5.5	5.242208	1025.4	1049.0	1082
k	5.280303	5.102273	1010.0	1037.0	1030.8
i	5.083333	4.977273	978.1	967.0	937.2
l	4.787879	4.925788	1013.5	1034.0	1043.6
g	4.454545	4.498268	876.1	755.0	844.1
e	3.931818	4.493182	921.6	931.0	920.9
c	3.772727	4.305844	948.9	800.0	896.6
d	3.613636	3.987121	866.3	735.0	820.1

Table 2: Win probabilities. This table demonstrates the win probabilities of each dyad, calculated in Rstudio given its own Elo-rating and that of its opponent. The table displays individuals on the *y-axis* and their probability of winning a dyadic interaction against individuals on the *x-axis.*

	a	**b**	**c**	**d**	**e**	**f**	**g**	**h**	**i**	**k**	**l**
a		0.758	0.974	0.985	0.93	0.707	0.982	0.855	0.911	0.864	0.867
b	0.242		0.892	0.929	0.781	0.438	0.919	0.639	0.741	0.655	0.659
c	0.026	0.108		0.591	0.322	0.082	0.563	0.189	0.277	0.201	0.204
d	0.015	0.071	0.409		0.244	0.052	0.472	0.133	0.206	0.143	0.145
e	0.07	0.219	0.678	0.756		0.176	0.733	0.338	0.449	0.354	0.358
f	0.293	0.562	0.918	0.948	0.824		0.94	0.696	0.789	0.711	0.714
g	0.018	0.081	0.437	0.528	0.267	0.06		0.149	0.227	0.159	0.162
h	0.145	0.361	0.811	0.867	0.662	0.304	0.851		0.614	0.517	0.521
i	0.089	0.259	0.723	0.794	0.551	0.211	0.773	0.386		0.402	0.406
k	0.136	0.345	0.799	0.857	0.646	0.289	0.841	0.483	0.597		0.504
l	0.133	0.341	0.796	0.855	0.642	0.286	0.838	0.479	0.594	0.496	

Table 3: Interaction matrix. This table demonstrates the number of interactions for each dyad.

	a	**b**	**c**	**d**	**e**	**f**	**g**	**h**	**i**	**k**	**l**	**Total**
a	0	2	5	4	1	5	0	0	2	0	1	20
b	1	0	3	3	1	2	1	1	0	0	0	12
c	1	1	0	6	1	0	1	0	0	0	0	10
d	0	0	3	0	1	0	0	1	0	0	1	6
e	0	0	1	1	0	1	0	0	0	0	0	3
f	0	1	1	0	1	0	11	3	0	0	0	17
g	0	1	0	1	0	0	0	0	0	0	1	3
h	0	3	1	0	1	0	2	0	0	0	1	8
i	0	0	1	1	0	0	0	0	0	0	0	2
k	0	0	0	1	0	0	0	0	0	0	0	1
l	0	0	1	3	0	0	0	0	2	0	0	6
											Total	88

Table 4: Elo-ratings. This table demonstrates the change in Elo-ratings for the duration of the study. Wins and losses causes the score to go up and down, respectively.

Date	**a**	**b**	**c**	**d**	**e**	**f**	**g**	**h**	**i**	**k**	**l**
Start	1000	1000	1000	1000	1000	1000	1000	1000	1000	1000	1000
6/8	1050	1000	1000	950	1000	1000	1000	1000	1000	1000	1000
6/9	1050	1000	1000	950	1000	1000	1000	1000	1000	1000	1000
6/10	1050	1000	1086	914	950	1050	950	1000	1000	1000	1000
6/11	1082	1000	1086	882	950	1050	950	1000	1000	1000	1000
6/12	1178	962	1028	882	950	1050	950	1000	1000	1000	1000
6/13	1178	962	1028	882	950	1050	950	1000	1000	1000	1000
6/14	1178	962	1028	882	950	1050	950	1000	1000	1000	1000
6/15	1178	962	1028	841	950	1050	991	1000	1000	1000	1000
6/16	1178	962	1028	841	950	1050	991	1000	1000	1000	1000
6/17	1218	962	1020	841	950	1063	1004	1000	1000	1000	942
6/18	1218	1070	1020	841	950	1010	949	1000	1000	1000	942
6/19	1240	1070	1020	841	950	1010	949	1000	978	1000	942
6/20	1240	1070	1020	906	852	1043	949	1000	978	1000	942
6/21	1240	1070	1020	861	852	1043	949	1000	978	1000	987
6/22	1287	1070	1024	832	852	1021	949	1000	978	1000	987
6/23	1287	1070	949	968	852	1021	949	1000	978	1000	926
6/24	1287	1070	949	968	852	1021	949	1000	978	1000	926
6/25	1304	1070	949	968	852	1004	949	1000	978	1000	926
6/26	1304	1070	949	968	852	1004	949	1000	978	1000	926
6/27	1304	1070	949	968	852	1046	907	1000	978	1000	926
6/28	1304	967	949	968	852	1046	907	1103	921	1000	983
6/29	1304	967	949	968	927	1012	866	1103	921	1000	983
6/30	1304	967	949	911	927	1012	866	1103	978	1000	983
7/1	1304	967	949	911	927	1012	866	1103	978	1000	983
7/2	1304	967	949	911	927	1012	866	1103	978	1000	983
7/3	1304	967	949	911	927	1012	866	1103	978	1000	983
7/4	1304	1014	902	871	927	1012	866	1103	978	1000	1023
7/5	1234	1014	1008	835	927	1075	866	1040	978	1000	1023
7/6	1234	968	1008	835	927	1075	866	1086	978	1000	1023
7/7	1234	968	1008	835	927	1075	866	1086	978	1000	1023
7/8	1234	968	1008	835	927	1075	866	1086	978	1000	1023
7/9	1234	968	1008	835	927	1075	866	1086	978	1000	1023
7/10	1242	968	1008	827	927	1149	823	1055	978	1000	1023
7/11	1242	968	934	901	927	1161	811	1055	978	1000	1023
7/12	1242	968	896	901	927	1161	811	1055	978	1000	1061

Table 4, continued

7/13	1255	968	867	901	914	1161	811	1084	978	1000	1061
7/14	1298	1039	867	909	914	1160	794	980	978	1000	1061
7/15	1298	1039	867	828	958	1160	794	980	978	1037	1061
7/16	1298	1039	844	851	958	1160	794	980	978	1037	1061
7/17	1311	1006	844	851	958	1201	786	980	965	1037	1061
7/18	1311	1006	844	828	958	1201	786	980	965	1037	1084
7/19	1311	1006	844	828	958	1201	786	980	965	1037	1084
7/20	1257	1060	844	828	911	1201	786	1027	965	1037	1084
7/21	1257	1090	892	780	881	1201	786	1027	965	1037	1084
7/22	1322	1090	927	745	881	1172	777	1027	965	1037	1057
7/23	1322	1090	927	745	881	1180	769	1027	965	1037	1057
7/24	1343	1113	882	745	881	1180	769	983	967	1037	1100
7/25	1343	1113	832	745	931	1180	769	983	967	1037	1100
7/26	1345	1142	803	743	931	1180	769	983	967	1037	1100
7/27	1345	1142	803	743	931	1187	762	983	967	1037	1100
7/28	1348	1150	800	735	931	1194	755	1049	967	1037	1034

APPENDIX B: FIGURES

Figure 1: Elo-rating visualization. This graph indicates the change in Elo-ratings over the study period. The blue dotted line represents the highest-ranked individual (DRa) and the yellow dotted line represents the lowest-ranked individual (DRd). The blue (DRf) and green (DRg) dashed line represents the dyad with the greatest number of interactions.

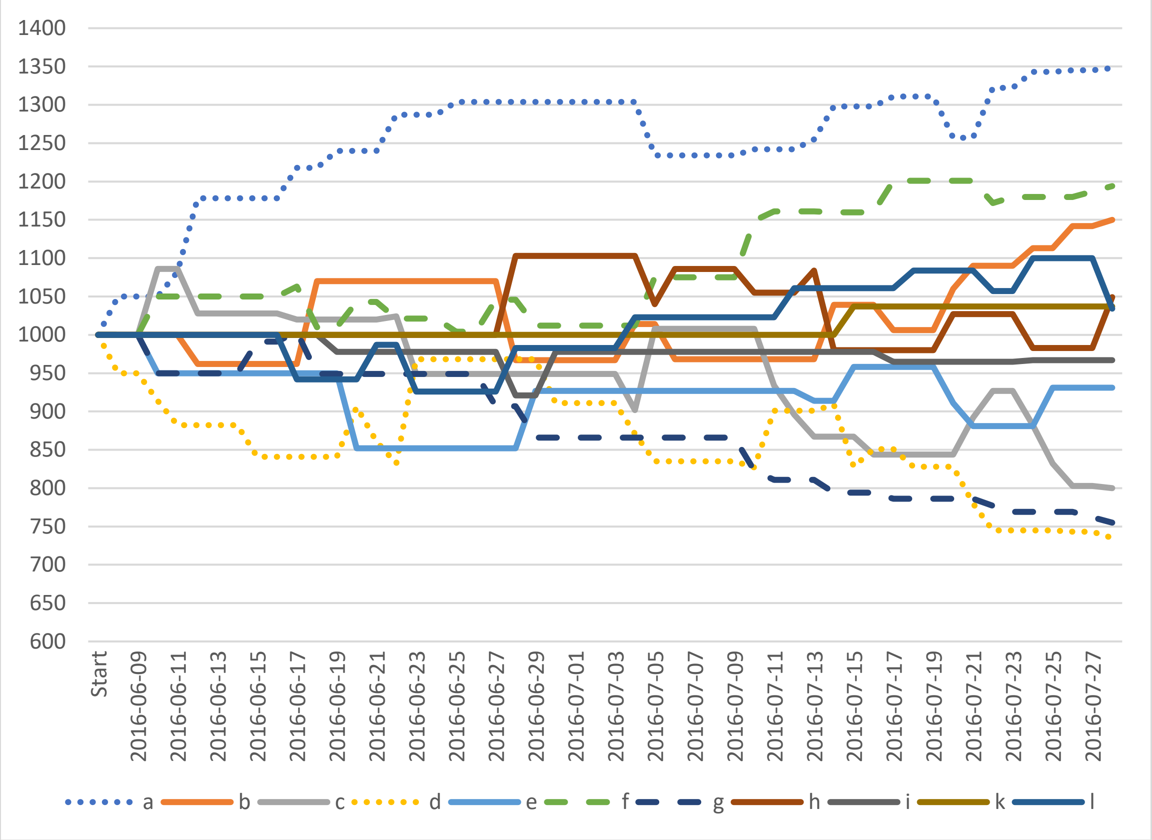


Figure 2: Distribution of interactions. This graph demonstrates the distribution of interactions among each dyad. Note that DRk had only one interaction over the duration fo the study. The highest-ranked individual (DRa) had the greatest number of interactions. DRf most frequently engaged with DRg, which were always seen together during the study.

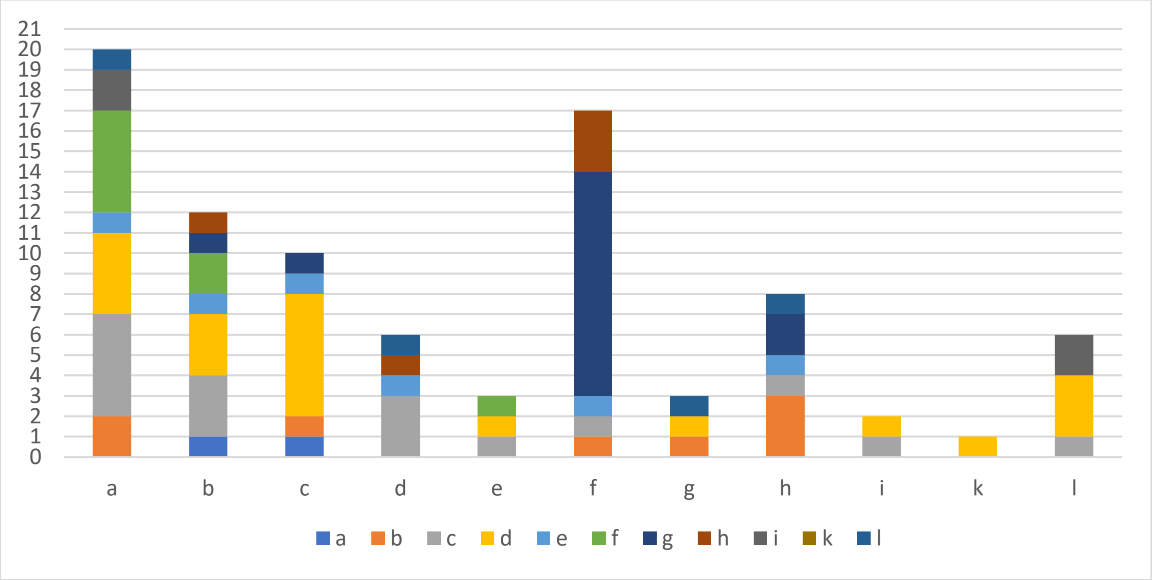


Figure 3: Hierarchy steepness. This chart displays the steepness of the hierarchy using both the observed normDS (P_{ij}) and the corrected normDS (D_{ij}).

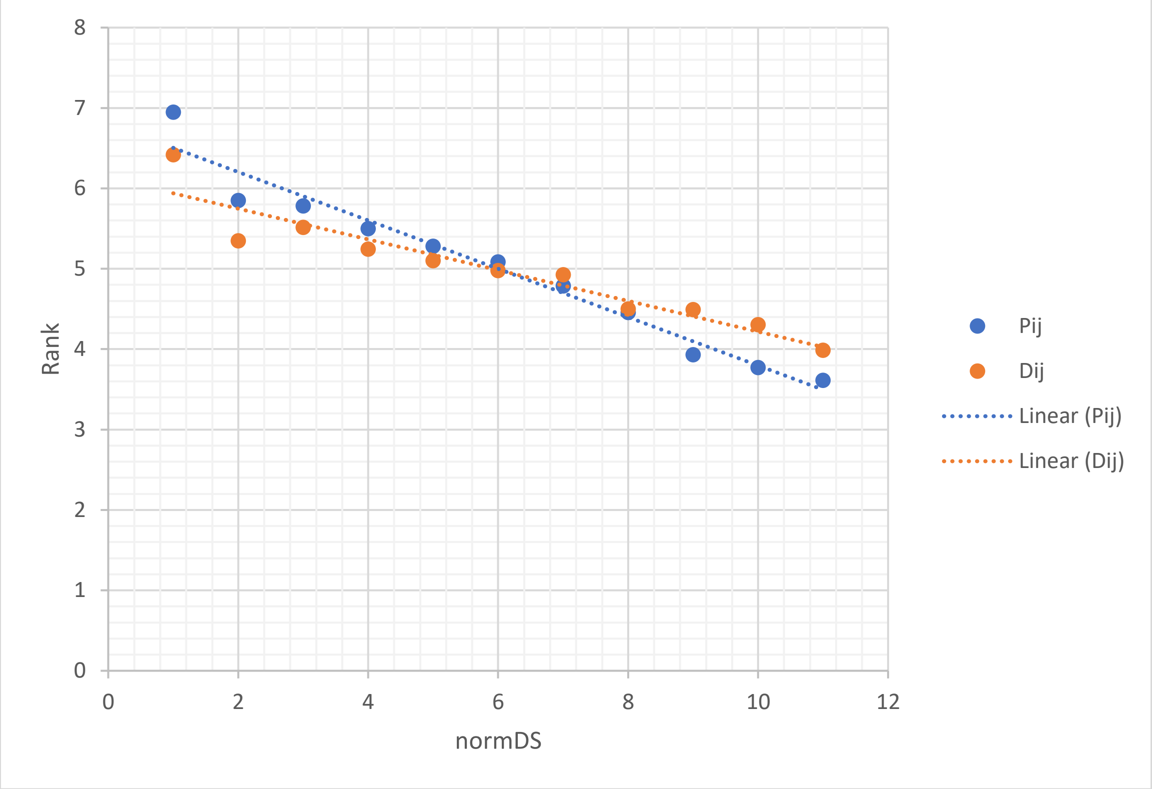


Figure 4: Win probabilities. This chart displays the win probability, given the final Elo-ratings, in each dyad according. Individuals on the x-axis are the potential victors and the y-axis displays the probability with 1 indicating a 100% chance to when an interaction. DRa is the highest-ranked individual and thus has the greatest chance to when in any dyad. DRd is the lowest-ranked individual and is least likely to win in any given dyadic interaction.

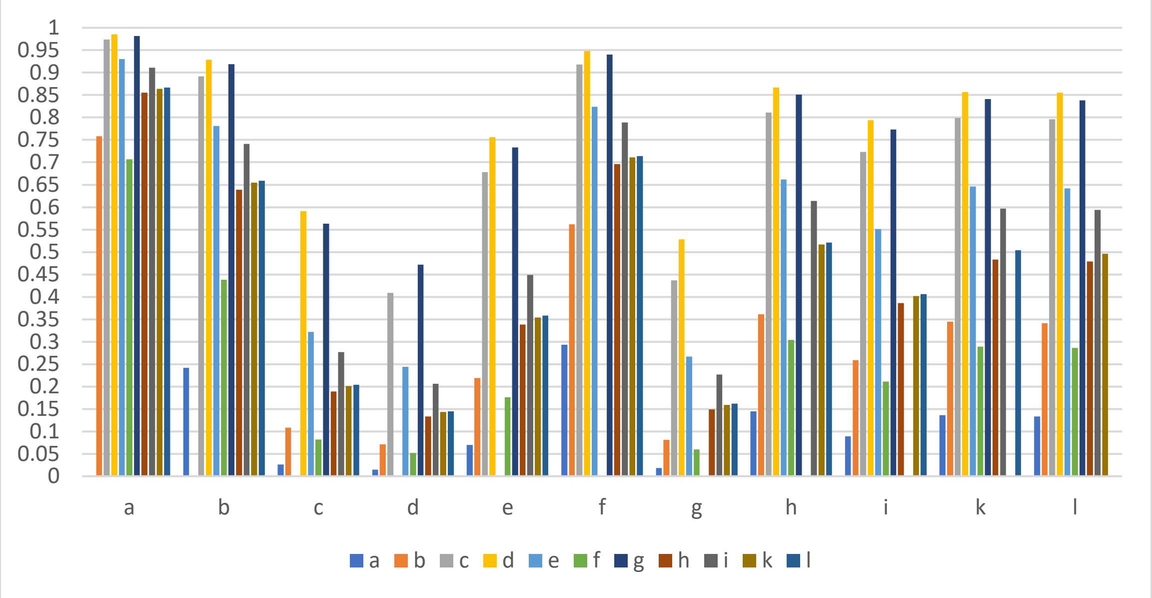


Figure 5: Study Area. The study area is located 1.2km northeast of Gores Landing, 9.15km southwest of Fort McCoy, FL. The study group is also about 14km northeast of Silver Springs State Park, the location of the parent population of rhesus macaques in Florida.

Figure 6: Activity Area. This maps demonstrates the activity area of the study group for the duration of the project. Red circles indicate June dates and yellow squares represent July dates. Sites that are marked by a tag indicate multiple-use sites.

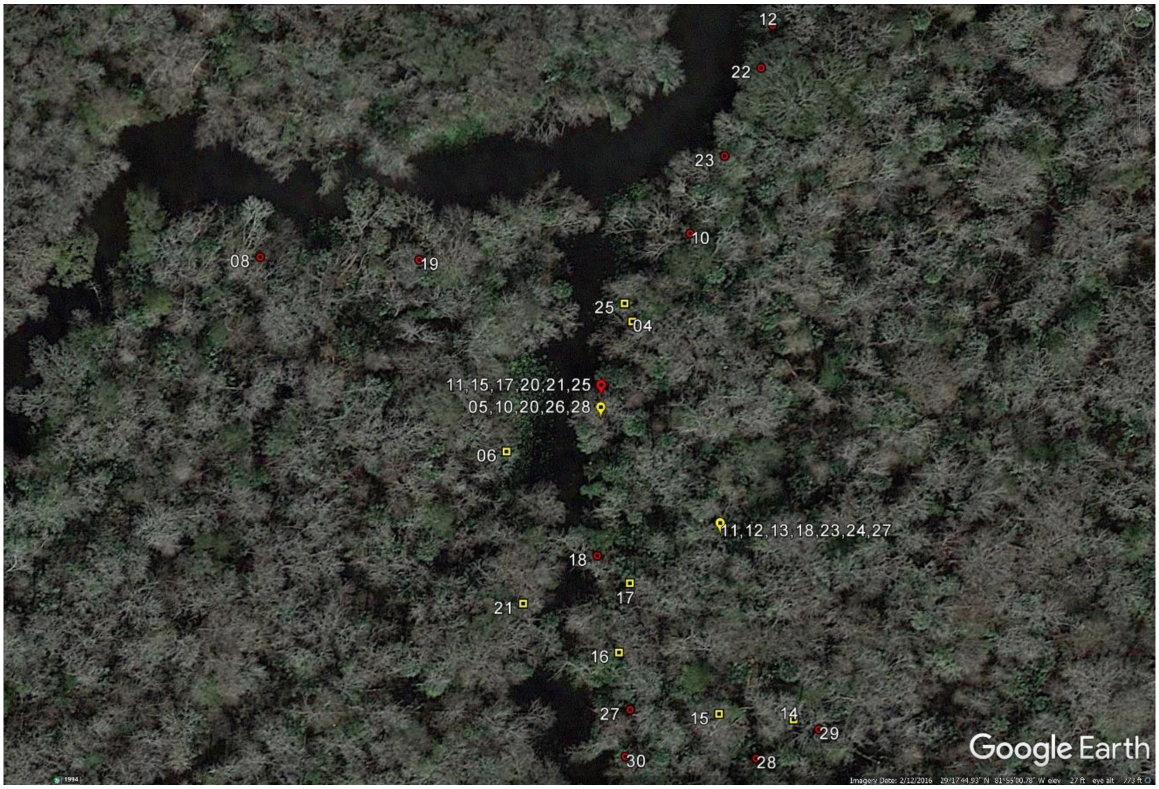
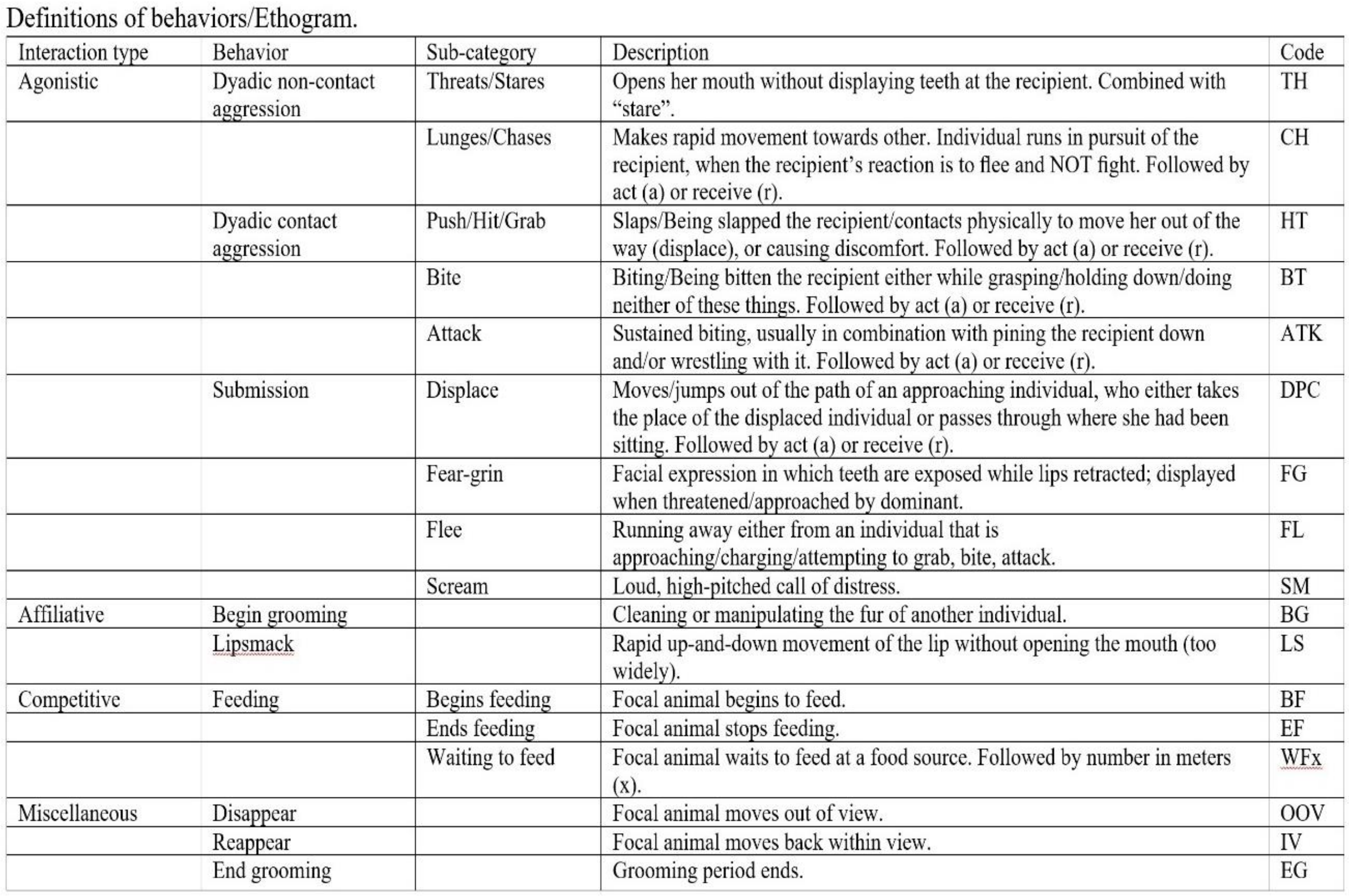


Figure 7: Ethogram. This chart includes the definitions of behaviors observed during the study period. Adapted from Balasubramaniam et al. (2014).



Definitions of behaviors/Ethogram.

Interaction type	Behavior	Sub-category	Description	Code
Agonistic	Dyadic non-contact aggression	Threats/Stares	Opens her mouth without displaying teeth at the recipient. Combined with "stare".	TH
		Lunges/Chases	Makes rapid movement towards other. Individual runs in pursuit of the recipient, when the recipient's reaction is to flee and NOT fight. Followed by act (a) or receive (r).	CH
	Dyadic contact aggression	Push/Hit/Grab	Slaps/Being slapped the recipient/contacts physically to move her out of the way (displace), or causing discomfort. Followed by act (a) or receive (r).	HT
		Bite	Biting/Being bitten the recipient either while grasping/holding down/doing neither of these things. Followed by act (a) or receive (r).	BT
		Attack	Sustained biting, usually in combination with pining the recipient down and/or wrestling with it. Followed by act (a) or receive (r).	ATK
	Submission	Displace	Moves/jumps out of the path of an approaching individual, who either takes the place of the displaced individual or passes through where she had been sitting. Followed by act (a) or receive (r).	DPC
		Fear-grin	Facial expression in which teeth are exposed while lips retracted; displayed when threatened/approached by dominant.	FG
		Flee	Running away either from an individual that is approaching/charging/attempting to grab, bite, attack.	FL
		Scream	Loud, high-pitched call of distress.	SM
Affiliative	Begin grooming		Cleaning or manipulating the fur of another individual.	BG
	Lipsmack		Rapid up-and-down movement of the lip without opening the mouth (too widely).	LS
Competitive	Feeding	Begins feeding	Focal animal begins to feed.	BF
		Ends feeding	Focal animal stops feeding.	EF
		Waiting to feed	Focal animal waits to feed at a food source. Followed by number in meters (x).	WFx
Miscellaneous	Disappear		Focal animal moves out of view.	OOV
	Reappear		Focal animal moves back within view.	IV
	End grooming		Grooming period ends.	EG