

Plastic Prosociality:
Conditions For Cohesion and Cooperation
in the Genus *Macaca*

by

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Class of 2015

A thesis submitted to the
faculty of Wesleyan University
in partial fulfillment of the requirements for the
Degree of Bachelor of Arts
with Departmental Honors in General Scholarship

Acknowledgements

I would like to thank my Thesis Advisor, Joyce Powzyk, for being such a wonderful, engaging mentor for this thesis. I greatly appreciated her comments and advice. My discussions with her have helped focus my thesis's intent while reminding me of the breadth of altruism's scope, as altruism is such a pervasive field of study. I look forward to taking what I have learned from her and applying it to future work and writing regarding primates, their behavior, and the environments they inhabit.

I would like to thank Professors John Kirn, Michael Singer, and Sonia Sultan for their assistance and advice in helping me find a route through which to write a thesis on primate behavior. Their suggestions were critical to my initial thought process and my decision to execute a thesis in General Scholarship.

Many thanks to the Registrar and Honors Board for creating and overseeing the Honors General Scholarship program. This has allowed me to pursue a thesis that would have otherwise not been possible.

I would like to thank all friends and family who have helped me in any way throughout this thesis process. Our discussions helped me find new routes to understanding and studying altruism and cooperation and have helped me fine tune this thesis. Your suggestions and encouragement have made the past few months go much smoother than I ever imagined they would.

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Introduction

While struggling to craft a hypothetical example that represents the complexity of primate behavior and how difficult it is for humans to interpret the meaning of these behaviors in a social context, I was suddenly blessed by the Internet. A trending news item graced the side of my Facebook: “Kanpur: Monkey rescues and revives companion after electrocution in Indian railway station.” In videos of this incident one can see a rhesus monkey poking, biting, and jostling an injured, unconscious conspecific who had previously been electrocuted by the wires above the train’s tracks (Red Kafal, 2014). Ultimately, the shocked individual was awakened and the other macaque stayed with the injured primate and proceeded to touch the individual. Meanwhile, hundreds of train travelers took out their cell phones to record the incident for all to see. It was noted that some viewers even cheered upon seeing the monkey stir (Waxman, 2014).

The capabilities of animal social behavior seem to capture quite a number of YouTube views. Kanpur is not an isolated incident for the reporting and recording of animal behavior. Not long before this news became viral, a story of a dog saving another pup’s life surfaced in Istanbul. Stories of unlikely friendships between members of unlike species become the basis for several television documentaries and children’s books. One popular example of this is that of Owen and Mzee, a turtle and hippo who co-habited and co-fed after the young hippo was orphaned. The co-feeding and mimicking behaviors seen between these two are wholly strange and call into question how a valuable relationship can be biologically defined and quantified. Also,

the popularity of these phenomena inspire because they provide hope for the notion that all crawls of life are capable of relative goodness.

Once these stories are brought out of the realm of “clickbait” and social media news, behaviorists, often specialists in the animal species at play, ruminate upon them, debating the validity of popular assertions that altruism and caring were present in these non-humans (Clark, 2014). Shortly after this piece of news surfaced, primatologist and TED-Talk extraordinaire Frans de Waal commented on the act of this macaque (de Waal, 2014). Some of the video’s comments argued that the purportedly altruistic actions were actually harmful, injuring the shocked monkey and placing him in precarious, dangerous positions. De Waal refutes these assertions, many of which address the macaque’s biting behavior. He notes that the biting behavior exhibited by the monkey creates contact solely with the incisors, preventing tearing of the victim’s flesh in a manner that resembles the nibbling behaviors exhibited during grooming in this species. Interestingly, his comments on the event in Kanpur have since been edited, removing his comments on the possible harm that the conspecific may have caused. Regardless, while this incident may inspire many to support and take pride in the kindness of animal (or mammal) kind, it cannot be determined whether this monkey would have regained consciousness otherwise and whether this lengthy period of interaction caused his re-animation.

However, the writings regarding the behaviors seen here forget to mention that during portions of this interaction, a third, conscious monkey was present. This monkey alternated between watching and disengagement, eventually leaving the train tracks prior to the injured monkey’s awakening. Why is it that this single monkey

chose to interact with this unconscious conspecific? Was the injured monkey kin? How do the social histories between the injured, aiding, and apathetic monkey explain these events? They certainly can explain more clearly than disgruntled YouTube commenters crying anthropomorphism. While seemingly helpful behaviors can be observed in wild, laboratory, and urban settings alike, the conversation should continually examine how these behaviors reflect the histories between individuals, groups, age classes, sexes, relatives, mates, and more.

In this thesis, I intend to propose that altruism and cooperation extend from two scenarios regarding the dynamics of groups: situations that promote the maintenance and preservation of present relationships and overall structure, and those that promote the dismantling of these relationships, altering the placement of individuals within social hierarchies and creating a different social system in which relationships and interactions are given newfound importance. In this way, the groups once described as being despotic can now be deemed ones that prefer social reformation, as lower-ranking members may form coalitions that allow for them to overthrow the highest-ranking male. Societies often referred to as egalitarian will be described in this model as being social maintainers. These groups behave in a way that results in few drastic changes in rank over time, though many subtle alterations of social hierarchy may regularly occur. The difference in fitness between high-ranking individuals and low-ranking individuals is small enough that aggressive, rank-altering behaviors are too risky for low payoffs.

By describing species within this framework, the onus of altruism is redirected to the environments that preclude social behavior. Also, by avoiding descriptors such

as egalitarian and despotic, the modest behavioral differences between species are given more ecological weight, and the differences are no longer seen as being determined by the presence or absence of despotic males. This definition will also better relate to behavior seen in females, as the previous terms primarily describe the dynamics and rank steepness of male group members. I also will address behaviors that have an ambiguous role in mediating pressures for maintenance and upheaval. This is particularly notable in play, as play behaviors can help perpetuate relationships but can often lead to the loss or change of valuable relationships when aggressive behaviors occur as part of play.

In this thesis, I will use research on the primate genus *Macaca* to demonstrate the dynamics of cooperation and how they differ depending on the variable environments and experimental conditions involved. Macaques are a diverse group of primates and form groups that differ with regard to how much power the group's alpha members have. Some species, such as the Tonkean, Tibetan, and Barbary macaques, are described as having egalitarian, tolerant societies in which the highest-ranking members are not so different from low-ranking monkeys. Other species, such as the rhesus and Japanese macaques, are noted as being despotic and totalitarian with regards to the import of the highest-ranking males (Thierry, 2000). In this paper, I hope that the aforementioned balance between social maintenance and upheaval helps address the many who describe the differences between these species as being derived from descent as opposed to ecological factors.

While these social differences are manifest through evolutionary history, the environment creates such a diversity of behaviors that the role of species in the

discussion of prosocial behavior is not always relevant or necessary. The despotic-egalitarian distinctions place social behavior under a highly deterministic framework that suggests less variation within species than between species. While many publications utilize similar experimental procedures to highlight differences between species, few acknowledge the differences in social behavior within a species. By acknowledging the plasticity of prosocial behaviors, these labels will less constrict the perceptions of these species' behaviors. After all, the monkey in Kanpur is a member of a totalitarian species, and yet the train context allowed for a profound act of altruism.

Biological Definition of Altruism

The word altruism stems from the writings of August Comte, who described altruism as sympathetic feelings (Scott & Seglow, 2007). These sympathetic feelings would be learned at a young age and allow for individuals to be “courteous” enough to function in a society that values “courtesy.” The individual behaves from these feelings in order to belong to the community and receive its benefits.

In a biological sense, altruism includes behaviors that increase the fitness of another individual at the expense of the fitness of the altruistic individual. This poses a problem for selection. As those who perform these behaviors will bear fewer young, how can these behaviors be selected for and develop over evolutionary time? As far back as Aristotle, individuals have considered the idea that people may do good things and consider the interest of others because, by being members of the same group, the interests of others are not unlike one's own. The most extreme example of human propagation of this idea is religion, as many creeds emphasize the importance

of and piety that comes with helping others. Hobbes secularized these ideas in making a virtue of egoism. One behaves prosocially because it is not only good for the group but oneself as well (Scott & Seglow, 2007). This can be seen in non-humans as well, as behaviors that provide benefits to others at a partial cost are eventually met with reward.

Many have looked to the concept of group selection in order to satisfy an evolutionary explanation for altruistic phenomena. In this group selection model, groups that contain altruists are believed to outcompete those that do not. By benefiting the needs of the group, the group may better persist (Wilson & Sober, 1994). However, some accuse this view of selection to be difficult, as altruistic individuals would still bear fewer young. Therefore, the altruistic membership of the group would eventually be challenged by the number of more fit, non-altruistic members. Though altruism may exist in groups, it would not be an evolutionarily stable strategy and would not persist over generations. However, this concept operates on the assumption that altruism is an inheritable, genetic trait.

Temperament differs wildly across groups within a species depending on the conditions of their birth and development. Feral housecats exhibit particularly different behaviors from those who are raised in a home and assimilated with humans. While all of these cats represent populations that bear the genetic marks of domestication, the difference in behavior stems from the environment. Occasionally, feral cats will assimilate into populated human areas, resulting in a calmer temperament stemming from habituation. Also, it seems likely that altruistic behaviors will be learned by successive generations and repeated with some degree of

generality regardless of kinship. In this way, the group selection model poses a greater threat to genetic determinism than altruism, emphasizing environment and learning over descent. Since altruistic behaviors have persisted, then these behaviors must, to a certain extent, be variably influenced by environment, such that self-sacrificing individuals have not disappeared from populations.

However, there is still great concern with how altruistic, cooperative behaviors can increase the individual's fitness and genetic contribution to the next generation. While certain sacrifices can be made at the individual's expense, these costs may be outweighed by benefits received by recipient kin. As these individuals share a certain quantity of the altruist's genes, then there is an ostensible level of fitness gained from the act. However, the less related the two individuals, the smaller the benefit to the compassionate individual. Hamilton aptly described how altruistic behaviors could be selected for with the equation $B/C > 1/r$, where B stands for the benefits of the act, C stands for the cost, and r stands for the degree of relatedness between the individuals (Ed. Wispé, 1978). If the benefits outweigh the costs proportional to the level of relatedness, then the behavior allows for an increase in fitness. This also means that more costly behaviors would be seen between highly-related kin compared to those seen between kin of little genetic relatedness.

However, this is not a complete view regarding the care seen in social species. Individuals will often behave prosocially towards non-kin. If altruism solely existed as a phenomenon between kin, then adult male macaques would exhibit virtually no altruism, as few adult males stay within their home groups where siblings would be

present. Also, these males would most likely be unable to provide care for their own offspring, as paternity is far from certain in macaque populations.

In response to this, social biologists studying these behaviors have deemed that reciprocity may be at play (Alcock, 2013). Reciprocity regards the suggestion that those who give may recoup their costs through receiving compassion in return. Biologists have parsed out reciprocity into three forms. I will use the example of grooming in order to illustrate these three routes toward reciprocity: direct, indirect, and generalized (Clutton-Brock, 2009). Direct reciprocity refers to an interaction solely between two individuals. Macaque A grooms macaque B; therefore, B grooms A in return. In indirect reciprocity, Macaque A would groom Macaque B, and Macaque C would groom Macaque A. Through indirect reciprocity, individuals who historically give, tend to receive more from other individuals. In generalized reciprocity, Macaque A would groom Macaque B, and Macaque B would groom Macaque C. Through generalized reciprocity alone, those who receive altruistic acts would tend to give more often than those who do not.

However, even reciprocity cannot fully articulate the dynamics of altruistic behavior, as certain acts cannot be reciprocated. This is especially true in humans. While adoption occasionally occurs within families, it is quite common that individuals will adopt completely unrelated individuals (Alcock, 2013). By planning to invest so much parental care in an unrelated individual, there is a certain level of non-selective behavior involved in altruism. This human example suggests that bonds can be made that have nothing to do with the fitness of the individual. However, it seems likely that the evolutionary steps that have led to such high levels of care for

kin have precluded this phenomenon. The ability and desire to give care has become lenient, allowing for individuals who spend vast amounts of energy and time to care for completely unrelated young. Conversely, some have described these benefit-less instances of altruism as being “induced altruism,” instances of prosociality that result from cues from the altruism-desiring individual. Though less common than the human example, this would also explain the few examples of adoption seen in the wild within primate species. In this way, the value of a relationship cannot fully be described by histories of reciprocity. Certain valuable relationships like that between parent and child can arise despite a lack of genetic relatedness. Adopted children don’t give obvious fitness benefits to their parents. Well, at least until retirement home visits and payments become routine during the adopted child’s adulthood.

There are also important findings regarding how endogenous mechanisms may affect prosocial behavior. Neuroendocrine systems are impacted by the behaviors of individuals. Monkeys who groom are shown to have decreased heart rates during their bouts of grooming (Aureli, 1999) while humans who give money to charity report having higher levels of happiness. Perhaps this is why the winter holidays present a kind of a peak for human happiness. Through this, it may be impossible to say whether the example of adoption presents no rewards in return for the caring parent, as they may receive endocrine gifts through their parent-child interactions. While it is difficult to incorporate the neuroendocrine aspects of altruism and its effects on the body into a framework based on a currency of resources and fitness benefits, I hope to address relevant neuroendocrine and physiological data wherever relevant. I also hope that future neuroendocrine research addresses

differences between low-ranking and high-ranking macaques. While a physiological relationship has been demonstrated, future experiments may determine whether high-ranking or low-ranking macaques show greater decreases in heart rate and stress hormone levels after bouts of grooming.

Another topic of note is how these behaviors are reflected by the individual's anatomy and physiology as evidenced by biometric data and blood and fecal samples. Biometric data may reveal how social organization is dictated by differences in size (Higham et al., 2010), as despotic societies may have males that are relatively larger than the alphas of egalitarian groups or may exhibit slightly stronger sexual dimorphism. Fecal matter allows for a non-intrusive glimpse at the neuroendocrine system as well as the dietary roles in the makeup of social organization. Very few studies reference these, and I hope future studies utilize these technologies in discriminating the origins of individual's rank and behavior.

Altruism and Economics

The topic of altruism in humans bears heavy ties with the field of economics. Human giving operates on levels quite similar to the routes previously described in non-human primates. Human groups show interest in the welfare of their groups, donating to local causes. However, group selection is tempered in humans through the many international aid efforts led by developed nations, showing interest in the welfare of members outside one's group. Humans are also heavily involved in the financial interests of their children, showing kin selection through their economic choices. By giving allowances to children and often substantially contributing to the fees involved in their college educations, there is tremendous financial effort in

ensuring the success and happiness of human offspring. Human financial endeavors demonstrate the concept of reciprocity, as dining companions alternate between who pays the check, and families exchange gifts during birthdays and holidays. There are many human expectations regarding whether or not someone should return these favors, and many economists have looked toward Darwinian, evolutionary reasoning in describing these phenomena.

Though Darwinian views of altruism have influenced the way we look at human economies and giving, there are also instances where economics can inform the way we look at non-human primate systems. This is apparent in studies on macaques and other primates where token economies are used (Bevacqua et al., 2013). In these artificial laboratory experiments, the test individuals can exchange tokens for rewards, most often food. In light of these studies, primatologists are more often considering non-human societies as having simple economies regarding the availability of resources. However, this requires the establishment of biological market theories that would describe and show the exchange between sometimes unlike services.

A paper on a “mating market” in long-tailed macaques, Gumert (2010) addresses the idea that male-female grooming may be tied to sexual activity in these primates, as grooming is timed to the receptive periods of the female and sometimes precedes sexual activity. By analyzing primate behavior and the notion of reciprocity in such a fashion, the relationships between interactors and interactions multiply such that goods can be exchanged in an abstract manner. For instance, males may be using grooming as a cover for all up close examination of a female’s reproductive status.

Grooming can preclude more grooming, sexual activity, food-sharing, coalition forming, lessened aggression, increased aggression, play, and many more social behaviors. By viewing social behavior within a market-place framework, prosocial behaviors can alter the social atmosphere and preclude a multitude of behaviors. Behaviors reflect not just momentary actions and reactions, but historical tendencies that depend on the individuals involved and behaviors that occurred well before the window of observation. While it is difficult to relate and associate behaviors due to the passage of time between events, addressing the history of interactors allows for a more complete understanding of how the behavior is meaningful and the extent to which the involved relationship is valuable within a social market. After all, non-human primates are known for their extensive memories such that they would have the ability to longitudinally reward friends and ignore (or aggress upon) enemies.

Human Psychology, Altruism, and Macaques

Popular social psychology works have shown that humans are often willing to help others and that certain variables increase the likelihood of altruistic acts. I hope to use these human examples to propose hypotheses for how human behavior can inform further observations. For instance, humans have been shown to be more helpful under circumstances of guilt (Stangor, 2010). This may manifest itself in macaques, as macaques that had been aggressive may reconcile with contact and grooming. Humans also are more likely to help those who are similar. This may present itself in macaques if individuals tend to groom and spend more time with group members of similar age class and kin circles. Another interesting concept is the idea of altruism as self-presentation. Humans are more likely to show their

compassionate behavior if this behavior allows for them to receive a good reputation for their kindness and charity.

The concept of an individual's reputation is particularly of interest to me, as this extends beyond the focus of much of the research I have seen in preparation for this thesis. While nearly all of these articles address the relationship between the altruist and the recipient, few papers address the presence of others nearby and whether the identity of those present bears importance. Could the presence of an "audience" bear weight in discussions of play between adult males and young? Present females may see this male-infant care and consider these playful, caring males desirable.

Another phenomenon discussed greatly in psychology is the finding that large group size can reduce the likelihood of intervention when conflicts occur. This has been popularly referred to as the bystander effect. When considering an audience effect in non-human primates, how does group size affect whether or not certain behaviors occur? For instance, if there is a conflict between two males, and there are several individuals nearby, how likely is it that another macaque will intervene? In the study of evolutionary behavior and psychology, researchers hope to determine whether these phenomena are at play in other primate species and in what environments do they occur.

Describing Macaque Societies

Through analyzing the differences in behavior between macaque species, some researchers have tried to parse out the origins of egalitarian systems that precede altruistic behavior. Some papers have suggested that higher intergroup

competition would result in populations that leaned egalitarian, as prosocial ingroup behaviors would be beneficial to outcompeting other groups. Others observed that the species described as despotic were less likely to exhibit prosocial behaviors between non-kin. Matsumara noted that the divide between these behaviors corresponds well with the family tree of macaques, such that “despotic” and “egalitarian” species lie separately on the evolutionary tree (Matsumara, 1999). Matsumara claims that it is important to note the evolutionary history when examining the behavior of macaques. However, the placement of despotic species on this tree raises the question of whether there were two evolutionary events that led to aggressive behavior. These correlations should not be confused with genetic, species-specific causation. The tree used in studies like Matsumara’s is telling of how populations diverged and found different spaces with slightly different ecological needs, resulting in more similar behaviors. Furthermore, it is important to note that hybridization is possible in certain systems. For instance, rhesus macaques and long-tailed macaques, both generally deemed despotic, share territory such that hybridization sometimes occurs (Stevison and Kohn, 2006). This occasional gene flow between these populations could be compared with their similarities in behavior. However, given their similar environments, it is important to recognize how all commonalities must be addressed in determining the origins of similar, potentially convergent behavior and dominance styles.

Other researchers have developed number systems in their descriptions of social organization. In this four-point scale, a score of 1 indicates egalitarian societies, whereas a score of 4 indicates despotic social organization. 2 and 3 indicate

moderate social organizations. While these descriptions allow for a more complete spectrum for prosocial and agonistic behaviors, very few species and groups are classified under these moderate designations. This leads me to believe that the extremes that 1 and 4 provide represent evolutionary stable strategies, whereas the intermediate values require environments where macaques are less commonly found. An evolutionary stable strategy is one that a group adopts that cannot be replaced by another alternative strategy given the same environmental conditions. In this way, despotism and egalitarianism may have become canalized such that drastic changes would need to occur for an alternative strategy to take hold.

Some articles have proposed a look at individuals in order to fully understand altruism, avoiding the generalizations regarding species and population when describing differences in behavior seen between “egalitarian” and “despotic” species. Hemelrijk addressed the need to note the behaviors of individuals and how the manipulation of individual social variables can affect several behaviors of other group members (Hemelrijk, 1998). Macaque societies are not static such that social organization is adaptive. Hemelrijk also noted that dominant individuals tend to remain in a more central position with respect to the group. Researchers have noted that lower-ranking males in these groups tend to wander more from the group’s center, often encountering individuals from other groups. While most behavioral information regards interactions between members of a single group, few studies address the presence of intergroup interactions and whether these are correlated with ecological conditions and whether the concept of a group should be questioned.

These are just a few examples of how the fluidity of social behavior depends

upon context. The low-ranking males do not migrate as a result of evolved, adaptive behavioral mechanisms; they do so because the central position of dominant males allows wandering behaviors to be more rewarding than maintaining a central position.

However, these views and the research that has been presented do not fully address the variation seen amongst the demographics of primate groups. The plasticity of social behavior shows that primate genetics in an evolutionary context only demonstrates how ancestral macaques separated. The genetic similarities seen between species of similar organization may merely reflect a history of similar environments. However, the environments they inhabit are fluid, and macaque behaviors change with respect to how the environment can provide for their needs. These needs continue to change to this day. While rhesus macaques that have virtually no human contact may be notably aggressive, the urban environments humans have created have formed a bastion for these monkeys that likely alters their behavior. The transition from woody foraging to finding scraps of food left behind by humans is a profound ecological change that likely decreases the pressure of finding food. The more docile members of these urban groups likely receive more food while the more aggressive ones dominate in the wild. A lessening of selection pressures derived from food foraging may drastically alter behavior and are likely to continue doing so. The more urban-dwelling rhesus macaque may begin to show more tolerant behaviors than its totalitarian sister species, the Japanese macaque. However, rhesus macaques that stay in wild locations may continue their “totalitarian” organization and lifestyle.

Strier addresses the phenotypic plasticity of social behavior, how the behaviors seen in macaques vary widely and without regard to family lineage (Strier, 2011). She notes that this plasticity is often apparent, as both individual and group behavioral trends differ depending on the context, determining whether cooperative or competitive behaviors are more likely. This plasticity in behavioral trends may not be adaptive in any way, as certain competitive behaviors result in failed attempts to increase one's rank and merely represent socially induced behaviors of statistically improbable success rates. One key ecological factor she addresses is sex ratio. If a group of monkeys increases its number of males, a number of behavioral pressures may change. First, as male number increases, the likelihood that male cliques will form increases. Cliques entail smaller groups of males that are more likely to groom, forage, and spend time in close proximity. While this allows for small-scale cooperative events, it may result in multiple high-rank males of great social value. As each small clique has its own dominant male, the aggressiveness of the group will lessen. However, this scenario may also lead to a decrease in availability of mates, increasing the aggressiveness of the groups. Also, there may be more inter-clique aggression than intra-clique aggression. Certain cliques may form historical relationships with females as well.

However, while Strier addresses the plasticity of primate social behavior and how fluidity of behavioral phenotypes is based on factors promoting competition and cooperation, she does not address whether these two concepts are mutually exclusive. Competition can often drive cooperation, as coalition-forming allows for greater competitive successes. In the case of a highly despotic male, cooperation may be

necessary in order for low-ranking males to adequately compete. That is why I plan to alter this paradigm in this thesis, such that the driving forces of altruism (as well as antagonistic behavior) are the factors promoting social maintenance and social reformation. Both maintenance and reformation can promote altruism, as both grooming and coalition-formation involve costs that may benefit others. However, antagonistic behavior is not without its ties to social maintenance. Many societies use antagonistic behavior in order to prevent changes with in-group dynamics. Despite their flattering descriptions, egalitarian societies have aggressive tendencies that help maintain group size and composition. Through aggressive behaviors towards new group members received during immigration events, groups can maintain the relationships at hand, such that each member keeps the valuable relationships it has without the interference of new parties.

Altruism's Messengers

E.O. Wilson and Richard Dawkins have contributed greatly to the conversations regarding the origin and preservation of altruism and cooperation and the dynamics that regulate social behaviors. Wilson described the nature of how social organization and its diversity can precipitate a number of new behavioral consequences in animals (Wilson, 2000). In this way, behavior is a product of its environment. In describing this relationship between behavioral diversity and evolution, Wilson describes the multiplier effect. As a result of having complex social organization, small evolutionary changes can result in much larger changes in behavioral patterns and social organization. The large differences seen between populations of different species are more regulated by social organization than by any

genetic mechanism. In describing this, Wilson calls attention to the olive and hamydras baboons. The two species show great differences with regards to their mating seasons, and consequently, social behaviors that occur during these seasons. However, when their populations overlap, interbreeding is quite common. In addition to genetic means of speciation, social evolution results in the separation of populations and their traits. This is an extension of environment's influence on behavioral and evolutionary changes.

This, however, does not mean that genetics are irrelevant to discussions of altruistic behaviors. In fact, for each of the social behaviors and tendencies Wilson describes, he imagines there would be genetic inputs regulating their existence and continued evolution. Dawkins idea of the selfish gene (Dawkins, 2006) has been widely associated with explanations of social behavior. By engaging in group living and participating in cooperative behaviors, individuals of these societies can increase their fitness and the amount of genetic material they can pass on to future generations. Through reciprocal and kin-directed behavior, genes have a better chance of surviving. In this way, the gene is active in altruism, as the individual who carries any given gene engages in these behaviors in order to increase the likelihood that these genes will be present in the next generation. While altruism's variation is a product of environmental and social inputs, its existence is a result of selfish exploitation of group living.

It is important to note, however, that these viewpoints were criticized by Wilson's colleague Stephen Jay Gould. He posited that Wilson and Dawkins writings relied too heavily on natural selection as the drivers of behavioral evolution and

change (Dugatkin, 2006). Furthermore he criticized such deterministic viewpoints regarding social behavior in animals, as these paradigms operate on assumption that social behaviors and organization are adaptive. While certainly some behaviors described in this thesis show strong evidence of being adaptive, as access to resources is granted to cooperative, altruistic individuals, it is wise to be wary and question whether social behaviors are necessarily adaptive and not simply baggage of solely their environments (without genetic input) and/or evolutionary history. While the multiplier effect is a powerful lesson in how small genetic changes can precipitate tremendous consequences, it is important to note that environments vary such that drastic phenotypic change is possible without any genetic change.

A More Amenable Altruism

The contemporary placement of altruism in biology reflects a history of envisioning altruism as adaptive behavior. However, seeing how different individuals behave altruistically at different times under different scenarios, altruism appears to depend far too much on context to be neatly described by an evolutionary tree. While altruism ultimately increases the fitness of others, there are so many paths that allow for the altruistic individual to receive benefit from their behavior. By seeing altruism as a product of a socio-ecological system, the descriptors “despotic” and “egalitarian” are no longer necessary as they suggest that groups are blindly following these paths and that these social systems reflect evolved temperaments across taxa. By describing these groups as those that exist under conditions that favor social reformation and social maintenance respectively, the environment gains more agency in these descriptions, and the place of altruism within any species’ preservation can be more

fully understood. Altruism can be seen as a means for survival that depends on social conditions that reflect an environment.

One need only look at the variability in humans to understand that descriptors of this quality are constantly under flux. For every Milgram experiment demonstrating that humans are capable of causing so much harm, there are others showing a capability for compassion. The seemingly most superfluous change in experimental methods can completely alter findings regarding social behavior. A similarly critical eye must be used when examining the works of altruism regarding macaques. The capability of increasing the fitness of others is highly present in primate lifestyles. By examining non-humans, it may be possible to better understand human behavior and where, when, and why compassion exists. While some macaques may certainly involve themselves in grooming more often than others, every macaque is endowed with hands with which to groom. All that is necessary is an environment (habitat and social peers) that allows the individual to scratch another's back, and an environment that has allowed the individual to learn that that they just might be scratching their own.

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Chapter 1

Returning the Favor

The Altruism Game

While many papers regarding the game theory and mathematics of altruism are filled with esoteric equations and theoretical dynamics of exchange, the seeming rules behind altruism remind me of a more tangible and popular board game: *The Settlers of Catan*®. In this game, players acquire and exchange resources in order to build roads, settlements, and cities. The game may elicit cooperation amongst players, as those who desire different resources can trade them so that both benefit from the exchange. Others can hoard their resources, making it harder for others to build and succeed.

While the resources involved in these board game civilizations are different from those necessary for the survival of macaque groups, the model seen here has inspired me to create and imagine a board game that can demonstrate how altruistic players can originate in a game with rules similar to those experience in macaque environments. I will list the instructions and rules here. First, each player draws a Rank card. The higher the value of this card, the higher in rank the player is. Each player begins by drawing an three of each type of resource card. The resource card pile includes Grooming, Food, Water, Space, and Sex cards. Once each player has received hir starting resources, the game begins.

The player with the highest Rank begins play, donating one (or more) of their cards to another player(s). Resource cards each have different values/costs (Resource Value). Once the player has given their card to another player, ze must calculate hir

score by multiplying the Resource Value on the card given with the Rank Score of the receiving player. It is important to note that the receiving player can either accept the given card or decline the offer, allowing players to shun others as part of their strategy. This number is the player's Social Product. In subsequent rounds of play, this number will be added to the player's pre-existing Social Product. The other players do the same, continuing in order from highest ranking to lowest ranking. During any round of play, it is possible for a player to abstain from donating any cards. At the end of each round, once all players have given cards, each player is allowed to exchange the Social Product points they received for more Resource cards. The players must pay the Resource Value noted for each card they choose. This payment reduces the player's Social Product score. Each player must have at least one card of each Resource in order to continue playing. Players that do not meet this criterion must forfeit the game and distribute their remaining cards to the remaining players as they so choose.

Social Product points can also be exchanged for increases in Rank Score. Though much more costly than Resource Cards, these exchanges allow for changes in rank amongst players. Unlike purchasing Resource Cards with one's Social Product, one does not take Rank points from a pile at the center of the table. Instead the player must take these Rank points away from another player. Two or more players can also spend their points together at a discounted price and equally receive the Rank points their target lost.

After ten rounds of play, each player totals their final score. The final score is calculated by the sum of their remaining Social Product and the total Resource Value

of the cards still in their hand. The individuals are then given their final dominance rankings based on their final scores.¹

With respect to this thesis, it is easy to imagine how such a game may result in patterns of social maintenance and social reformation. Relationships may begin to form, promoting a social environment of maintenance, as players who have historically received resource cards from another player will tend to give cards back. In some cases, players may abstain from saving their Social Product scores in order to increase their Rank scores. As doing so would require a player to refrain from purchasing resource cards as much as fellow players, a player hoping for Rank gain could lag behind players who continue to involve themselves heavily in resource giving and trade. Competitors who recognize that the selfish player is planning to trade Social Product for a Rank gain may refrain from giving resources to this player, making it all the more difficult for the player to have cards to give in order to increase his Social Product score. Selfish individuals may eventually be met with reward in some cases; however, the group of players may punish the player's actions, making it difficult to do so.

This is reminiscent of research involving food sharing in rhesus macaques. One paper on this species (Hauser, 1992) demonstrated that those who do not vocally announce their food discoveries tend to receive more aggressive behaviors than those who cooperate with the group and vocalize upon finding food. As seen in the wild behavior of this species, the Altruism Game allows for players to punish those who

¹ It is important to note that if the game's players collectively determine that the game is unfair and cease their playing, they are all declared winners, as this realization demonstrates the fact that they realize that their cooperation is ineffectual in ensuring a fair game for all. In a sense, these players can be considered the most cooperative.

try to behave selfishly and cheat the system while giving social benefits to those that cooperate with others.

Two factors that may affect the behavior of players in a similar manner to the effects of social organization in the wild are group size and the skewness of Rank score between players. If groups are relatively small, this increases the likelihood that large differences in rank may occur. These large differences in rank may force the low-ranking players to behave more selfishly in order to have even a slight chance of success. Also, despite the random nature of the drawing pile, it is possible that the choice of these cards provides for a playing group that disproportionately contains high-ranking or low-ranking members. Sometimes, if the playing group lacks mid-ranking players, the dynamics involved may be highly skewed, as low-ranking individuals receive few benefits from the cohort of high-ranking players who tend to affiliate only with one another.

Another concern regarding the highest-ranking players is whether or not a cap should be placed on Rank value. As these players are valuable, they will likely receive a lot of cards and give a lot of cards, allowing them to increase their Rank score dramatically at the end of turns. As this is an unfair mechanic for the game and does not accurately represent the fluidity of social organization seen in wild primates I propose that such a cap exists. However, choosing such a cap is a difficult task, as it imposes a maximum for resource dominance, a trait that would be highly variable in comparing wild species. How much higher in rank can the highest player be than the lowest player while still maintaining realism with regards to the real-world model provided by wild macaques? If this discrepancy is large, then it can become difficult

for low-ranking individuals to succeed without increasing their Rank score. However, if this difference is only slight, changes of Rank score, become virtually unnecessary, as strategy begins to focus on giving and acquiring what is necessary in order to survive, often forging social histories in order to ensure this survival. In this scenario where differences between players are slim, social maintenance behaviors become strategies for success and survival.

In this chapter of my thesis, I will discuss behaviors that are often associated with social maintenance. These behaviors that do not often precede changes in rank include grooming, food-related behaviors, and anti-group-predatory behaviors. While grooming behavior accounts for any prolonged tactile contact between two macaques, food-related behaviors can range from simply cohabiting the same feeding area to vocalizing about food locations to laboratory experiments in which individuals actually hand food to others directly or through a token economy. In each of these behavioral discussions I will note how these otherwise costly behaviors can lead to increases in fitness for the altruistic individual but will also address the irrationalities and idiosyncrasies presented by these behaviors and the research involved. Many of these behaviors demonstrate how group living precipitated the origin of these behaviors and their benefits, wild observations occasionally suggest how selfish interests prevent behaviors from reaching their maximum altruistic effects.

Grooming

Grooming and Kin Selection

While juveniles are quite obviously affiliated with their care-giving mothers and maternal kin, precluding behaviors such as grooming, it has been shown that even paternal relatedness correlates with closer interactions. Even though these siblings do not have a mother in common, providing socially enforced affiliation, their relatedness regulates their behavior through some mechanism for recognizing general genetic relatedness. Widdig et al. (2001) showed this in their study on females in a population of *Macaca mulatta* (rhesus macaques). Examining the behavior of these females and assessing their relatedness through DNA tests, the authors demonstrated that, while the relationships between maternal half-sisters were the most profound, resulting in the most behavioral events, these female macaques preferred interacting with paternal kin over non-kin. It was also demonstrated that these effects were greater when paternal kin were more similar in age, with the effect diminishing to no effect when age difference exceeds one year.

This relationship makes me question the extent to which this study's data may simply show that those who were fathered by the same macaque in similar years are likely to join similar social cliques within the entire group. While the researchers suggest that these relationships stem from kin recognition sensory systems based on morphological or endocrine similarity, it could also be associated with the finding that paternally related sisters may occupy adjacent positions within the female social hierarchy. These researchers did not address rank in their work, and accounting for rank may minimize the effect solely established by paternal kinship. Another question I have in regards to research on kinship is how kinship effects reciprocity. While literature on kinship and reciprocity are abundant, the bulk of publications I have seen

tend to address one or the other and not their interactions. While macaque females are more likely to interact with their paternal sisters, is it true that most of these cases of grooming and other behaviors are reciprocated? If so, is reciprocity more consistent in dyadic interactions of kin than non-kin? Are there differences in whether interactions are reciprocated between paternally-related kin and maternally-related kin?

Grooming and Reciprocity

As mentioned before, grooming is often reciprocated, and different paths toward reciprocation can occur (direct, indirect, generalized). One study examined all three of these possible routes to reciprocity and noted that direct reciprocity was the only route that bore power as a statistical predictor for the occurrence, duration, timing, and frequency of grooming events (Majolo et al., 2012). However, some indications of indirect reciprocity were shown, as third party group members were quicker to groom those who were grooming than those who were not. It is important to note that this did not result in a higher frequency of grooming for groomers than control individuals; there was simply less latency or a faster response time. The authors noted that this may be due to indirect reciprocity's cognitive demands, as it would be cognitively difficult to infer that those who give grooming would give such services to oneself. However, this may simply be more a product of conservative behavior and energy management, as those who groom these historical altruists are not certain that they will receive grooming in return. The histories of these individuals must be accounted for, as third party observers may also recognize that they are not likely to receive grooming from those involved in the present interactions.

Cooper and Bernstein (2000) analyzed the social behavior of *Macaca assamensis* (Assamese macaques), noting how the grooming behaviors in this species reflect reciprocity and social bonding hypotheses. In the case of this species and their study group, reciprocity was demonstrated; however, instances where general grooming trends were biased in certain directions based on sex and rank were noted. For instance, subordinate males groomed dominant males more than these high-ranking group members groomed them back. Females, rather, tended to groom subordinate males more than these low-ranking males groomed them back. Also, both sexes groomed subordinate females despite the observed lack of reciprocation exhibited by subordinate females. Though the previous examples demonstrate examples of reciprocity in the wild, the presence of imbalances in the reciprocation across affiliative networks demonstrates the importance of the social cohesion between unlike groupings. For instance, male individuals likely receive indirect benefits from subordinate females through social cohesive effects.

The authors of this paper address the matrifocal nature of this species in discussing the nature of this imbalance in heterosexual grooming. By grooming subordinate males, females create a social environment in which the subordinate males are more likely to stay. In this way, grooming can go outside the bounds of reciprocity ensuring the stability of the group's membership. Also, I would like to add that by increasing the likelihood that the males stay, the females' behavior may induce a more competitive environment due to the large number of immigrant males that choose to stay and mate. Through creating this competitive environment, females can be more choosy and maximize the health of their potential offspring.

Another grooming relationship that shows little reciprocity as evidenced by this paper is that between adult males and juveniles. As these males cannot distinguish which males are kin and these juveniles do not groom back very often, other social forces may be at play. Though the authors do not suggest why males may groom these juveniles, it may be that these behaviors maintain affiliative networks between males, as these youngsters will eventually become adults. However, the authors did not note whether the juveniles groomed more often by males were male or female. This is a critical distinction to make, as adult male relationships with juvenile males may be less important than those with juvenile females. As these juvenile males are likely to leave the group during adolescence, these females are more likely to share a social environment with the adult males and may, once sexually mature, be potential mates. Other hypotheses regarding male grooming of juveniles would suggest that those who do so are more likely to mate with females, as females see this behavior as desirable. However, a relationship between juvenile affiliation and mating success has not been supported by data in the wild.

Grooming and Mating

Gumert (2006) demonstrated the first analysis of the relationship between grooming and mating in a primate species. His surveys of long-tailed macaques showed that grooming precede mating events. This was only the case for male-to-female grooming. Rank was also incorporated into this exchange, as high-ranking males groomed females comparatively less prior to sexual activity, and high-ranking females were groomed more extensively than low-ranking females. In addition to the function of female-to-male grooming in ensuring that the male population stays

within the group and is likely to protect offspring, Gumert suggested that perhaps grooming is reciprocated if sex with the grooming partner is not desired. By grooming these soliciting males, females prevent a mating event as well as potential aggression from the male.

By grooming these females, males are more likely to access mating opportunities, but also receive information about these potential mates. However, this does not devalue the function of grooming as a precursor to mating. Like in human dating, partners invest time in one another in order to better understand their qualities as a mate and inciting continued courtship if desired. Males may also, by spending time with females and monopolizing access to females, reduce the likelihood that other males will be able to form consortships with these females. Perhaps these males' success with female macaques results from the physiological results of grooming. By lowering their stress levels (or the stress levels of female recipients), these males are more capable of mating with these females. However, unlike examples seen in other primate species, these macaques did not demonstrate grooming timed with the receptivity of the female.

Through these pathways, grooming between the sexes allows for the greatest success in mating seasons. Male-female grooming events provide knowledge for both partners involved, socio-sexual security for males, allow for more precise choosiness on the part of females, and create a social environment that allows for higher quality mating events. While these behaviors are costly, they ultimately result in social and reproductive benefits. In order for this to be true, the rate of success must allow for benefits that exceed the costs. Gumert noted that higher-ranking males groomed less

and spent less energy on the females they mated with. However, despite the suggestion that this dynamic would preclude an environment where high-ranking males mate with other high-ranking females and low-ranking males would mate with low-ranking females, incongruities occur. Low-ranking individuals mate high-ranking individuals of the opposite sex and vice versa. By studying the nature of these incongruities and whether these mating efforts are successful, the biological mating market can be better understood. If low-ranking males continue to groom high-ranking females even though they are virtually ineligible mates, there must be other factors inciting these grooming events.

Grooming, Sex, and Rank

The previous examples in this chapter demonstrate how the pathways to altruism (kin selection, reciprocity, and group selection) are affected and complicated by their interaction with biological sex and rank. Some general trends have been noted: in Tibetan macaques it was found that male-male grooming was related to dominance rank and histories of less aggression between individuals while female-female grooming was more associated with reciprocity and adjacent rank membership (Xia et al. 2013a, Xia et al., 2013b). These differences in grooming within the sexes are quite revealing of how life history and environment influence behavior. Female philopatry results in female relationships that are more cooperative and less dependent on temporary resource needs, food and females, unlike more competitive, aggressive male macaques. This may suggest that females are less likely to be social reformers, as they are less likely to seek rank-related benefits by affiliating with and grooming dominant group members (Macdonald et al., 2013). Some authors have

suggested that learning may also play a role, as juveniles learn to allocate grooming resources by watching and mirroring their mothers. Female juveniles more frequently mirror their mothers' behavior and also begin initiating bouts of grooming at an earlier age than males (Mayagoitia et al., 2010). For these philopatric females, becoming a valuable member of the natal group is highly desirable from an early age.

Manson et al. (2004) have addressed the interaction between reciprocity and dominance rank in females in bonnet macaques. These researchers demonstrated how dominance rank differences between grooming partners influences whether reciprocity occurs and the duration of grooming that occurs between these partners. When the macaques involved in the grooming interaction were balanced with respect to rank, reciprocated grooming was more likely to be similar in duration to the initial bout of grooming. However, the correlation between rank and time-matching (equivalent durations of reciprocated bouts) was less profound in macaques compared to another studied species of non-human primate, white-faced capuchins, a New World monkey species. It may also be noted that capuchins were far more likely to reciprocate during grooming bouts, as only 5-7% of bonnet macaque dyads showed reciprocated grooming within a single period of interaction.

While the relation between rank and grooming time is indicative of how grooming depends upon a relationship's value, the data regarding bonnet macaques may show a stronger reaction if longitudinal data on separate grooming bouts between the same pairs were considered, disregarding whether or not the behavior was reciprocated within an individual period of interaction.

It has also been shown that grooming soliciting behavior has different effects depending on rank status and kinship (Ueno et al., 2014). While soliciting behavior is equally likely to be met with a grooming response in non-kin and kin subordinates, it was demonstrated that dominant individuals were more likely to respond to soliciting behavior of kin than non-kin. This study on Japanese macaques shows the dynamics involved in social relationships and rank. As subordinates are more likely to benefit from grooming any individual and maintaining that social bond, there are fewer incentives for a dominant individual to groom a group member who is not related. These members may reciprocate their grooming to this dominant member; however, these subordinates likely would groom this dominant regardless. While dominants can be choosy with regards to whom they groom, subordinates benefit from any social contact and have no incentive to be selective.

This study also noted that members that are unaffiliated non-kin (those who do not typically interact with one another) were less likely to respond to a solicitation behavior if they had not already been groomed in the first place. While the dominance relationships demonstrated above is relevant, it could be that dominant members may tend to be less affiliated with subordinates if they are not kin. Social affiliations may be more lenient in subordinate populations. While this relationship between affiliation and response is well articulated, showing this effect across quartiles of dominance rank may show variability with regards to the effect of solicitation.

The Physiology of Grooming: Altruism and Anxiety

As I noted in the introduction, altruistic behaviors often affect the physiology of the organism, affecting neuroendocrine pathways and heart rate. As grooming

potentially decreases stress hormone levels and heart rate, some have considered that grooming and other prosocial behaviors might be routes to decreasing anxiety. These social acts reduce buildup of stress hormones, as the social cohesion the act provides is rewarding to the individuals involved. It is important to note that these studies differ with regards to their scope. While heart rate information and behavioral data reflect immediate responses to grooming, chemical samples from blood and feces must be compared with general trends in grooming. (Who historically gives and who historically receives?). Some have gone so far as to say that, with regards to grooming, it is “better to give than receive” (Shutt et al., 2007). However, recent publications on stress-related behaviors following and preceding grooming events suggest that grooming induces a stressed state (Semple et al., 2013). Nevertheless, the chemistry of altruism is important to address, as it may reveal how stress stems from social scenarios and how this stress can be behaviorally reduced. Through the study of these effects, one can determine whether giving’s costs are immediately met with a physiological reward and how these rewards depend upon the grooming event’s context.

The incongruity between endocrine benefits has been demonstrated in Barbary macaques, a notably egalitarian species. This study showed that those who groomed to more individuals and groomed for longer periods of time had lower glucocorticoid levels in the fecal samples collected (Shutt et al., 2007). Since these stress hormone levels simply show that those who groomed more individuals and more extensively were less stressed, the mediating factor could be social organization. Those who are more heavily involved with more members of the group show lower stress. Grooming

is a social tool that may lead to familiarity with more members of the group and a more accepting social environment that may result in lower stress levels. Conversely, those who are less stressed may be the individuals that groom more, as these individuals would be less afraid to interact with other members of the group. If this is so, those who groom will continue to groom, as the physiological result of grooming perpetuates a state that precludes grooming in the individual.

It was also shown in rhesus macaques that grooming allows for greater decelerations in heart rate (Aureli et al., 1997). As this study broadly addressed social interactions' effects on heart rate, it demonstrates grooming's role in eliciting a parasympathetic response while other social encounters increase heart rate and cause stress. For instance, it was shown that encountering a dominant individual increased heart rate significantly for both young and adult macaques. However, unlike the previous study, in which the effects were shown in the giver of grooming, this heart rate study reflects the recipient's reaction to grooming. Given this framework, it could be possible to imagine how dominant males can exploit this in some groups in order to maintain their rank within the group through social interaction. While their presence may elicit increases in heart rate, their grooming of subordinates could potentially allow for faster decreases in subordinate heart rate that allow for the formation of trust from subordinate individuals.

Two recent articles (Molesti and Majolo, 2013, Semple et al., 2013) addressed self-inflicted scratching after grooming bouts suggest that post-grooming anxiety may occur. This anxiety has been shown to not correlate with the likelihood of aggressive interactions after bouts of grooming. It has also been shown that this self-scratching

behavior is more common in the recipient than in the giver. The hypothesis regarding this self-directed behavior does not necessarily seem to reflect the anxiety of the recipient. When humans receive haircuts it is common for them to touch their hair after the event, getting used to the new shape of their tresses and making it feel comfortable on their head. Certainly, I often scratch my head subconsciously during periods of stress, but I can imagine that distinguishing the intention of these two acts could be difficult. Scratching behavior seen in macaques could simply be that the act of being groomed results in the recipient's interest in their own fur.

It was also noted that the self-directed behavior was relatively high before the act of grooming. In this way, this scratching may be received as a message to a nearby group member, asking for and prompting a grooming session. The behavior seen after the grooming episode could be the individual's attempt to solicit another groomer or to urge the original groomer to continue their bout. As mentioned before, certain postures and behaviors precede and solicit the act of grooming. While this behavior may arise in other situations that are known to cause anxiety. However, these cases do not reflect what has been demonstrated in the previous papers regarding heart rate and reflect the tenuousness in assuming an emotional state from a generalized behavior.

Grooming: A Caveat

While these examples show how grooming is a costly behavior that stems from an evolutionary need to form relationships with group members. However, the concept of grooming-related feeding tempers the idea of grooming as an example of altruism. On occasion, grooming individuals will find pests buried in the fur of the

other monkey and consume these insects. In this way, grooming could actually be seen as a selfish act. Some have gone so far as to describe feeding and pest-removal as the primary functions of grooming. This conclusion was founded on the observation that nearly all (98.9%) pieces of food that Japanese macaques find and consume during acts of grooming are parasitic pest insects (Tanaka et al., 1993). Regardless, this act inadvertently helps the receiving individual, reducing the presence of lice in their lice. However, this draws into question the origins of these behaviors. While not all grooming events result in feeding, did the altruistic act of grooming stem from this selfish feeding behavior? Or did grooming develop in evolutionary time as an altruistic behavior that occasionally results in opportunistic, selfish feeding?

However, the anecdote of Lp, an observed Japanese macaque, provides an example of how the need to feed and the beneficial effects of grooming present trade-offs (Onishi et al, 2012). Lp is a female Japanese macaque whose fur was severely affected by parasitic insects. She was groomed more often than any other member of her group, as this grooming allowed the groomer to feed on the lice present in her fur. However, while this allowed for Lp to be healthier than she would be if she were not groomed, the consideration of grooming-related feeding resulted in moderate grooming-related feeding. As a result of this moderation, lice eggs remained in the fur such that the pest population would remain in her fur. If more feeding occurred, this would not maximally benefit the groomers, as the population would be exterminated and grooming-related feeding would no longer provide benefit to the groomer.

Feeding Behavior

One behavior that sometimes occurs after grooming is co-feeding. It may be obvious that those in close proximity (as often is the case after grooming) would be close enough to feed in one another's presence. However, given the general trend that macaques do not often feed with one another, it can be said that affiliative behaviors are powerful tools that allow individuals to feed socially and, potentially, reap some nutritional rewards from doing so. For instance, female Japanese macaques feed more often in the presence of those with whom they groom, reinforcing their preexisting social relationships while furthering foraging abilities (Ventura et al., 2006).

Feeding is a highly social behavior in primates. Those who find food often do so in the presence of others. Sometimes, when they find this food independently, they vocalize to others in order to inform group members that food has been discovered. In this way, macaques and other primates do more than simply tolerate the presence of others at a feeding site; they encourage it by soliciting others nearby. However, food, as it is so necessary to the survival of the group, can also be an important social tool. By living in groups, individuals are more likely to know where food is, as this knowledge can spread between individuals through their behavior. Individuals can allow feeding or deny it to others depending on the context: whether the individuals differ greatly in rank, have a history of aggression, or are in the process of courtship.

Studies have shown that feeding behavior is learned from one's kin. In a study on Tonkean macaques, it was shown that matrilineal groups differ with regards to the eccentricities of their feeding behavior (Drapier and Thierry, 2001). For instance, some macaques did not eat the skin of apples provided to them while others

did. While much of the feeding behavior was common between these matrilineal kin networks, the subjects showed novelty behaviors that reflected their familial network of infant learning. While these behavioral variants show no likely differences in fitness, it is very important that these youngsters eat in a social environment, as their mothers demonstrate how one should eat, what one should eat, and how to find it. Adult macaques also depend on others in order to acquire food. While they forage with greater independence than infants, they learn about the locations of food and acquire feeding strategies from group members.

A famous example of this is that of the female Japanese macaque who initiated a novel feeding behavior that propagated throughout the group. This macaque began to utilize the nearby water for nutritional benefit; she began washing her sweet potatoes (Nakamichi, 1998). In doing so, the vegetables would then contain some minerals from the saltwater while potentially removing any grime and dirt that had come into contact with the vegetables. By throwing these grains of rice into the water, the macaque also avoided consuming dirt. While pecking at grains of rice amongst grains of sand requires a great amount of work, throwing these grains along with sand allow monkeys to take the floating pieces of rice while the dirt sinks to the bottom. This behavior soon spread to other members of the group, allowing them to reap the benefits of her methods. In fact, new behaviors with similar results began to take hold, as some individuals began to use stone to a similar effect, peeling dirt off of their root vegetables. The multiplier effect is again at play through social behavior. As behaviors exist in a social realm of learning, repetition, and change, their

evolution and acquisition of new pathways and functions is incredibly speedy and adaptive.

By eating in a social group, these monkeys were able to acquire this new technique. The very social nature of feeding allows for greater success than if it were not. Meanwhile, there are a number of instances where the social nature of feeding can be manipulated or even more immediate in its consequences. While eating in the presence of others is important to understand, the more costly acts of sharing with others are relatively rare phenomena that help support the benefits of sociality as well as altruism. While the example above does not show altruism, it is indicative of an environment where feeding allows for periods of extended contact between group members that allows for transactions between unlike members of a group. This giving of information may essentially be passive, but can be costly. By revealing the location of food to others in the group through the act of foraging, one loses some access to food that could otherwise be one's own. However, being in a social environment, this is not necessarily a bad thing. As tolerating the arrival of incoming feeders may strengthen the ties between group members, allowing feeding time to maintain these bonds and reiterate the benefits of the individual's place within the social hierarchy.

Sociality and Feeding: Benefits of Prosociality and an Egalitarian Style

Sociality has effects on the way groups forage, and these different techniques show variation across species. A study on Japanese macaques has indicated that co-feeding has a positive influence on food intake and the amount of time spent at a site (Kazahari and Agetsuma, 2008). This result, however, does not comply with conclusions drawn in other publications that have shown that separate foragers spend

more time at individual food sites. In order for this to happen, the group must avoid the phenomenon of scramble competition that would result from resource depletion. Scramble competition refers to the phenomenon in which a finite resource (here, food) is equally shared until it is depleted. However, this information suggests that, while the ecosystem seen here presents patchy food sources for these macaques, there are enough patches to avoid instances of competition. In addition to avoiding negative effects of competition, aggression did not have an effect on food intake and other feeding metrics, as aggressive behaviors were rarely seen from dominant individuals.

Even in this “despotic” species, the benefits of social cohesion are quite apparent. Co-feeding allowed for more optimal foraging, increasing the food intake for the group’s members. Some authors question whether this is evidence of sociality increasing individual’s ability to forage, suggesting that the increased food intake may be a response to the presence of others. Co-feeding introduces an element of competition, resulting in more hurried feeding. Another hypothesis regarding this suggests that foraging efficiency can be facilitated socially, as laboratory experiments have demonstrated that individuals will eat more when other feeders are within sight.

The author’s final hypothesis regards the idea that feeding with others is simply more time-consuming, as individuals who wander from the group do not have to spend time and energy waiting for and reuniting with group members. Social cohesion is, in this way, inefficient. However, a more recent study (Kazahari et al., 2014) produced by the same research team has demonstrated that the residence at food sites is more intimately associated with the group’s need for social cohesion than maximum intake rates and optimal foraging. Members of a foraging group spend less

time at patches when they have little social proximity to group members and longer periods when nearby others. Feeding behavior may be governed less by physiological needs than social needs.

Group size is a substantial factor in determining the nature and dynamics involved in feeding, determining the extent of competition as resources are limited. With regards to competition surrounding food, large groups demonstrate greater intra-group competition while smaller groups demonstrate more inter-group competition. While these groups did not differ with regards to the frequency and presence of aggressive behaviors associated with feeding events, the larger groups, by nature of their lack of inter-group competition, have better access to high-quality resources. Even subordinate members reap the rewards of this lack of competition. However, smaller groups do not have this luxury. As a result, dominant members of these groups are more likely to have access to the highest quality food sources.

While these behaviors are likely mediated by the social organization and relationships of and within these groups, it is important to note that there may be a level of feedback here, as food competition influences the way group members behave with one another (Majolo et al., 2009). Feeding dynamics may have an effect on behaviors like grooming which, in turn, foster a social environment in which certain pairings are more likely to behave tolerantly and co-feed. In instances where inter-group competition is great, groups (especially their female members) may adopt tolerant behaviors in order to better defend their resource patches. In the case of groups where intra-group competition is great, a more despotic organization may be noticed.

It is important to note that these observations were made in nearby groups of the same species. These two unlike groups represent the variability of social organization and how it reflects ecological pressures. This flexibility of behavior demonstrates the idea that giving species such titles provide statistical generalizations about the behavior of entire species that are primarily based on populations that have been historically observed and easy to access. For instance, much of the work on rhesus macaques is performed on a Puerto Rican island where they have been introduced, Cayo Santiago. As rhesus macaques are native to southern Asia, this environment is likely to differ from that seen in their original habitat. These differences likely have an effect on the behaviors seen. However, many publications regarding the macaques of Cayo Santiago claim the despotic nature of this species on this island despite this island's sometimes abnormal group sizes and compositions. In order to fully address the behavioral ecology and dismantle these terms, it is critical to understand the many environments that have defined the totalitarian behavior of the rhesus macaque.

Group Feeding: The Benefits of Tolerance

A recent study in Japanese macaques has demonstrated the benefits that come from feeding in a group (Otani et al., 2013). The study showed that individual foraging is less successful than foraging in groups, resulting in a lower rate of feeding. The authors did, however, suggest that these individuals do so in order to alleviate the competitive pressures that come with feeding within the group. Low-ranking males were more often found ranging separately than high-ranking, as they are likely to receive aggression when foraging with the group and, therefore, less

likely to receive food. In this way, though those who feed with the group show higher rates of intake, the low-ranking individuals who are likely to separate from the group could potentially receive less food in this context.

This poses a problem for cooperation. While many reap the benefits of this cooperative act, others cannot infiltrate this social system such that food intake can be increased. Though the behavior of the high-ranking core group is a good example of cooperation, these few are excluded because of their rank. This suggests that cooperation has upper limits. While travelling in a group increases the rate of discovery, after a maximally efficient group size has been attained, additional members only decrease the share of others while providing a small increase in the group's ability to forage. However, the authors have posed an ecological consideration. When certain foods are abundant and lie central to the group's range, there is lower likelihood of separation in feeding on these fruits. Due to a decrease in competition for this food, there is less of a need to separate. As this research is on Japanese macaques, a despotic group, it would be worthwhile to compare the distribution of food plants in this species with an egalitarian group. It may be that egalitarian systems rely more heavily on abundant plants, allowing for lowered competition and greater inclusion of low-ranking individuals in group feeding events.

It is important to address how animals are socially kept within feeding groups and what precedes group feeding. It has been shown that grooming often precedes co-feeding between macaques. As this behavior supports social cohesion, it seems possible that grooming can be exchanged for an episode of tolerant feeding. Feeding fits in a reciprocal framework, as it can be included in exchange pathways seen in the

wild. Those who tolerate co-feeding are more likely to be allowed to feed with these group members again.

It is also important to note that co-feeding is a behavior that is developmentally regulated, as juveniles exhibit these behaviors first with their mothers and, later, with their peers (Ueno et al., 2005). This was demonstrated in research on Japanese macaques that showed that juveniles and yearlings are more likely to begin feeding when those near them are doing so as well. In the presence of adult group members, these individuals only begin to feed when others do so, ensuring that the food is desirable and that they will not be aggressed upon. In this manner, group feeding is critical, as it enforces a structure in which like individuals find safety for finding good food and also ensuring the success and survival of one's juvenile affiliates.

Co-Feeding and Consorting

Another situation where co-feeding is tolerated is in the context of mating events. In a study on rhesus macaques, mating dyads were compared with male-female pairings that had not mated (Dubuc et al., 2012). The mating dyads were more likely to co-feed than those that had not. While I have addressed how co-feeding can be seen as a mechanism similar to grooming in its increasing social tolerance and cohesion, the authors suggest here that social tolerance is what allows for co-feeding. The social tolerance seen in their study stemmed from the context of consortship. In this way, levels of social tolerance that would allow for group feeding are exceptional (at least for rhesus macaques).

However, it is important to understand what allows for this difference. Do males actively lessen their aggression to allow for co-feeding, or do females become more bold and become less fearful of co-feeding with these males? As it is possible that these females will bear young in the months after these events, it may be a physiological reaction to need to feed after mating. Needless to say, this paper addresses the finding that feeding and social behavior are regulated by the context and whether relationships are valuable enough to allow for the tolerance's costs. As this co-feeding behavior appears to be a product of the consortship, it would be worthwhile to compare these findings with what one would see in other macaque groups that vary with regard to sexual pressures. In those found in scenarios where there are more males, it seems likely that males would invest more time, energy, and tolerance into these females in order to ensure consortship.

Food Sharing

It has been noted that high-ranking individuals are more likely to grant access to food than those of low rank (Massen et al., 2010). By allowing this access, these individuals stress their importance to subordinates. Subordinates can then attempt to remain in the favor of the dominant individual and reap the benefit of food access. One experiment on feeding was conducted in a laboratory setting, in which monkeys were able to grant food rewards to monkeys (of the same sex) in adjacent cells. In this way, though previously cited works demonstrate a lack of prosocial behavior on the part of dominant individuals, prosocial behavior in feeding allows for these monkeys to maintain their position through the control they have over resources. While grooming may be a tool used by subordinates to gain acceptance from higher-ranking

individuals of the same sex, feeding may exercise a role in ensuring the leader's position, offsetting the costs of acts like grooming and rendering behaviors like grooming necessary for receiving food and surviving.

Publications have hypothesized that food-sharing is affected by kinship, as the sole instance of food-sharing in wild macaques is between mother and offspring. This relationship, however, does not translate to an increased likelihood that individuals will yield food resources to kin in a laboratory setting. However, one study demonstrated that a few factors increase the likelihood that individuals will yield food to kin relations (Schaub, 1996). Three of the eight female long-tail macaques in this study gave more food to kin, as these test individuals were presented with very young kin. Very young kin are believed to be the most common recipients of kin assistance, as their survival most depends upon the help of others. It takes a village to raise a child; this proverb bears no less weight in a network of related female macaques.

While instances of food sharing are induced in laboratory conditions and virtually are non-existent in the wild, they represent kin-related tendencies and suggest how the dynamics involved in tolerant co-feeding may have been precursors to natural food sharing demonstrated in apes (including humans). However, these examples of sharing do not necessarily demonstrate altruism. Giving of food can often reduce costs that would result from not yielding food to a solicitor, as the costs being aggressed upon may inhibit individuals from feeding efficiently if at all.

However, there are forces that drive instances where individuals will even remove food from the mouths of kin in a phenomenon known as food-snatching (Hadi et al., 1996). These behaviors, oddly enough, are often directed towards

juveniles, being subordinate and easy to steal food from. While taking candy from a baby seems like an easy and cruel behavior, the occasions in which mothers will do this to their own young suggests otherwise. Perhaps giving their young food only to take it away from them allows mothers to know how well their offspring are able to chew their food or they may chew further in order to give the food back to their ineffectually masticating infants. Further investigation may show diversity in the function of food-snatching behaviors. Regardless, food snatching is an example of food's dynamic role in social behavior of various relationships.

The Case of Deception: Vocalization and Information Withholding

While the examples above demonstrate subtle ways in which the social system of macaques creates an environment where prosociality results in greater feeding, there are examples of active food-based altruism in the wild. One example of this is vocalization, in which animals announce the discovery of food so that others can arrive and share this food. This is a costly behavior, as the finder reduces his or her share of the discovered food. It has also been shown that those who do not announce their discoveries are sometimes punished by their groups. In one study on rhesus macaques (Hauser 1992), it was observed that those who did not vocalize received more aggression than those who did not. It was also noted that females who called upon discovery ate more food than those who did not. This could be because group members chased those who did not vocalize upon being discovered with unannounced food.

It was also noted that females were more likely to call than males. This is relevant to the forces that may underlie this behavior. Females are more related to

group members as a whole, so this announcement of food would more likely attract group members who are related. The paper also noted wild observations in which individuals are more likely to call when food is abundant at the site of discovery. By increasing the size of the find, vocalization becomes more likely, as even large shares of the cache allow for ample eating.

However, it must be noted that the experiments involved in this study, in which human researchers dropped food for discovery, took place in a central position in the studied group range. While call rates may typically be high when they occur in an area where group members are likely to be found, this may not represent what one would see in the wild. As noted previously, group members often forage separately from the group, where calls would be unnecessary, as no one would be able to hear them. This also addresses the notion that the study's findings may better explain the behaviors seen in egalitarian groups where separate feeding and wandering locomotive paths are less common. Also, it is important to consider how the identity of the discovered food may influence behavior. It was noted that calls were more likely for coconut, a more nutritionally desirable treat, than for monkey chow.

However, this study, though showing the costs associated with deception, does not mitigate the reality that food-related deception is a widespread phenomenon in macaque groups. One study examining dyadic effects on feeding related behavior in Tonkean macaques only once observed macaques informing others of food locations (Ducoing and Thierry, 2003). While dominant, informed individuals did not alter their behavior with respect to the rank of the naïve participant, it was noted that these individuals traveled more quickly to the site of the food when in the dyad than

when they traveled alone. This is likely due to the finding that the traveling companion may consume the food if they do not travel speedily. In a “tolerant” species, there is greater chance that subordinates will press their luck and deny a dominant individual access to food.

Informed, low-ranking subordinates, however, were shown to withhold information given that they were paired with an individual much higher in rank. The authors suggest that these individuals, from experience, know that they cannot normally receive food when paired with such asymmetrically dominant individuals. In these instances, the low-ranking individuals would not behave normally, increasing their sudden pauses and travelling more circuitous routes to the source of food. While these tactics are certainly not fool proof, by tiring the dominant follower and responding appropriately to the follower’s behaviors, it appears that these subordinates who do so increase the likelihood that they will receive a food reward.

While these deceptive behaviors are selfish, they demonstrate methods by which egalitarian societies regulate uniform food intake across its membership. In the case of deception-related aggression, those who do not behave prosocially are punished. However, these deceptive behaviors allow for subordinates to obtain food in scenarios where dominant individuals would usually have control over food patches. Also, though the group may enforce cooperation through aggressive means, deception is far more likely (and beneficial to the deceiver) in these unlikely cases of strongly asymmetrical pairings. Given that individuals will most likely forage with others of similar rank, the need for deception is little. In this way, the aggression seen in deceptive acts does not necessarily indicate the group’s ability to punish

withholding information, as it also holds a function in punishing subordinates who have been trying to feed with individuals of much higher rank. These behaviors allow for social maintenance and the perpetuation of relationships, as aggression is used in order to establish rules regarding who should be able to forage with whom, a feeding hierarchy based on rank and social history.

Odor-Matching

Another mechanism that allows for macaques to understand where food is located is through odor-matching or visual cues. Much of the research on social cues that allow for easy food discovery has been conducted in Tonkean macaques (Chauvin and Thierry, 2005). It has been observed that these macaques will occasionally sniff the chewed contents in a conspecific's mouth in order to determine what food is nearby and be able to find it. It was also noted that the speed at which the sniffer then forages depends upon the value of the food that they have recognized through olfaction. However, while food quality could be assessed through this odor-matching behavior, the macaques did not significantly increase their foraging speed when the conspecific had discovered a large food horde. In this way, olfactory information can only signal the quality of the food, not the quantity.

Another study showed this in a laboratory setting, although the food transfer was done through a human researcher (Drapier et al., 2002). Macaques were only rewarded when they approached the human experimenter who was positioned next to the food that the conspecific had consumed. These monkeys were then conditioned to recognize and remember the foods conspecifics presented to them. While this paper addresses the concept of odor-matching, this experiment also showed that macaques

could visually determine the location of high value food from a conspecific. This was done with a Plexiglas sheet that prevented the macaques from sniffing one another's food discoveries. There are multiple routes through which macaques can passively transfer this information.

It has been said that these passive acts of information transfer cannot be considered altruism. There are virtually no costs to this behavior, but they do allow benefits to others that can be lessened through deception. In this way, the absence of deception suggests the presence of cooperation in this species. For instance, the individuals involved in these visual and olfactory cue experiments could deny the inquisitive conspecific this information. While the hungry participant may try to smell the contents of the other's mouth, this monkey could deny this by keeping their mouth closed or fleeing. While the lack of costs seen in this behavior indicate a lack of altruism, they demonstrate cooperation, as this behavior requires tolerance on the part of the chewing individual. One paper addresses the lack of cost, calling it the non-human equivalent to eavesdropping. However, given that acquiring olfactory information with accuracy requires the monkey to sniff the other's mouth, it seems possible that the other is aware of the olfactory information transfer and tolerant of its occurrence.

I also must note that the tolerance seen here could stem from the experimental conditions. First, the macaques had assimilated to the experimental conditions during a training period, allowing them to form associations with potential odor-matching partners and preferences for certain foods. It may be of interest to future study of odor-matching to observe this behavior in the wild and see if it is prevalent only in

dyads that have an extensive social history or are members of the group at similar rank levels or of the same sex, allowing researchers to understand who makes a good odor matching partner. Also, it was noted in one study that different food preferences could arise for different individuals. While 27 out of 30 macaques preferred a strawberry to a menthol reward, this does not deny the finding that some preferred the menthol. In studies where food choice is not random, it is important to note this. Few studies have addressed individual preference, and it may be critical to the study of feeding behavior to note whether preference and dietary gradient correlate with rank.

Following the Leader: Cooperation and Judging Information

One study in Tonkean macaques demonstrated not only how information can be exchanged between individuals, but addressed whether individuals may have the ability to discriminate between different messages about food (Ducoing and Thierry 2004). Macaques, when faced with different information regarding food from two group members must discriminate between who has the tastiest treats. In doing so, however, their choice is often guided by the behavior exhibited by those who have already discovered food. In this way, though two individuals may be attempting to lead the naïve individual to a source of food, the macaques are able to agree upon a path, more often than not choosing the more rewarding path to food. In doing so, the individual informed of the lesser food site must not only recognize that the others is better (by observing their behavior), but also must concede to the other individual and not receive their own more certain food reward. Though deception is a distinct phenomenon in macaque communities, a sense of trust is seems to be both present

and common, as individuals occasionally will give up their own food sources in order to respond to other group members behavioral signals.

Eating and Conflict

Feeding poses some issues for prosocial behavior. As resources decrease and populations rise, conflicts can occur when too many members choose to feed at a single patch. However, it has been shown in female Assamese macaques that feeding behaviors tend to avoid these conflicts (Heesen et al., 2014). Females tend to react well to these ecological conditions, choosing to search for another patch when too many individuals are situated around one and eating with one's social members. While this segregation may sound like a departure from the descriptor egalitarian, this separation into social circles is critical in avoiding aggressive behaviors during feeding and also correlates with a decrease in rank-related differences in food intake. This leveling of food intake appears to be allowed through low-ranking members' more regular use of their cheek pouches. By storing their food, they are better able to exploit their resources to their advantage. The authors suggest that primate species that lack food pouches would demonstrate more feeding-related aggression.

Alarm Calls and Mobbing Behavior

The most costly of all altruistic behaviors seen in primates involve the threat of predation. Studies have shown that primates and other mammals have developed complex vocalizations that inform nearby group members of the presence of a predator. These complex sounds inform not only the presence but also the identity of the animal in certain cases. By informing others of the presence of predators, these

individuals become more noticeable and increase the risk of being attacked by the predator. However, in actuality this behavior decreases the likelihood of attack, likely as a result of a behavior called mobbing that is often associated with alarm calls. Predators that hear the alarm may retreat. However, this only seems likely in mammalian predators that would be able to hear these frequencies (leopards, but not pythons).

In mobbing behavior, group members respond to the alarm call by coming close to the threatened individual. By increasing their numbers, the group becomes better able to fend for itself and increases potential danger for the outnumbered predator. For instance, if macaques mob toward the alarm caller, a leopard may realize that their potential meal reward does not exceed the risk of being attacked by these defensively aggressive monkeys. Sociality again allows for better survival of the group in this case. However, there are cases in which this behavior is truly risky, as those who respond to mobbing behavior can become injured or killed during an attack. In the case of alarm calling and mobbing, though the behavior allows for survival, the risk of death, though low, is profound enough for this behavior to be called altruism (as opposed to cooperation) in instances of high threat.

There are a number of factors that must be examined to better understand this phenomenon. First, given that macaque species give different vocal responses depending on the species of animal, do nearby conspecifics respond differently depending on species-specific perceived threats? It must also be considered whether the identity of the caller (infant or adult, kin or non-kin, subordinate or dominant, male or female) and the identity of those nearby affect the call's response.

Kin and Rank Caller Effects

A study in crested macaques has examined the relationship between callers and responders in a laboratory setting (Micheletta et al., 2012). Test subjects were played recorded alarm calls that were recorded by experimenters in trials where individuals discovered a model python. It was found that these females responded more to calls of affiliated group members than non-affiliates. This response was measured by the amount of time that the subject was oriented toward the speaker playing the call. However, the researchers showed that the response was almost immediate regardless of the identity of the caller. In this way, though all calls are equally received, calls of affiliates are given more attention and time on the part of the listener. The researchers note that this greater attention may translate into what would be increased likelihood mobbing in response to an affiliate's call. As affiliates depend upon one another for social support and are likely to share resources, the costs of mobbing outweigh those of losing an affiliate. However, in order to validate the suggestions of this paper, such a relationship would have to be seen in a wild. Though these relationships would be harder to parse, as once mobbing occurs there are multiple relationships one needs to analyze across the mobbing group, it would be important to note the order of response and what this says about the social cohesion of all those who responded as well as those who heard the call and did not commence mobbing.

However, this study also noted that these female's responses showed no correlation with differences in rank between the listener and the identity of the recorded caller. As crested macaques are unanimously dubbed an egalitarian species,

the role of social affiliations exceeds that of rank. It may be that there is a stronger rank effect on mobbing behavior in species that are dubbed despotic. However, these may also be perceived as being associated with social affiliation. In these species, response to calls may decrease as rank difference increases, as individuals are more likely to have social affiliations with members of the group who are closer in rank.

Age and Calling Behavior

Observations in the wild have noted that individuals are more likely to respond to the call of an adult than the call of a juvenile (Ramakrishnan and Coss, 2000). While this may seem like a heartless disregard of the welfare of the group's young, given that these responses correlate with social affiliations in the group, it logically follows that juvenile calls would be less provocative. They have fewer ties to the group, as most of their behaviors are directed towards their mothers and sometimes siblings. Another explanation for the weakened responses to juveniles is that juveniles are more susceptible to a wider variety of species, some of which would not present a danger to other macaques. This has been demonstrated in the alarm calls of vervets, but has not been demonstrated in macaques.

Also, these young individuals may also be less reliable than the calls of adults. The behavior of adults suggests issues with reliability when responding to the calls of infants. One paper (Ramakrishnan and Coss, 2000) showed that adults spend more time evaluating the dangers of a situation when responding to the call of an infant that has been played through a speaker adjacent to a model of a leopard. In doing so, it could be said that this ensures that costly responses (like mobbing) are only executed when the situation has been perceived by the responder.

This study also demonstrated that subadults and juveniles are more likely to respond inappropriately to auditory stimuli. For instance, juveniles and subadults are more likely to flee upon hearing the sound of a motorcycle than adults. Also, these juveniles did not fail to respond to calls of adults, as all study subjects (both juvenile and adult) responded to playbacks of adult calls. However, juveniles were more likely to respond to calls of younger individuals, suggesting that juveniles are either less able to discriminate adult and juvenile calls while also supporting the notion that juvenile calls address a wider array of species. As juvenile responders may be able to discriminate the species noted in the call, the need for flight in juveniles is more necessary. Therefore, response to any such stimulus may be necessary for survival.

While the lack of response to juveniles may demonstrate a lack of caring for the group's youngest members, responses to juveniles were not void of altruism. The delayed responses merely allow adult responders to ensure that the costs of responding will be offset by a present danger. Also, while it was addressed that individuals observed in this study were placed into categories based on both age and sex, no results were shown regarding the differences in response between adult males and females. It may be noted that females are more likely to respond to juvenile calls, as they are more likely to be kin given the group's multifocal lineage.

The Interaction of Threat and Response

The strategies involved in escaping prey depend upon the animals involved. A recent study has explored the differences in rhesus macaque behavior that depend upon the abilities of pursuant predators. The three types of predators utilized in these experiments are felids, raptors, and snakes. While felids and raptors are capable of

swift flights to predation, snakes move rather slowly such that danger is less severe. Studies have shown differences in the acoustic structure of calls depending on species (Coss et al., 2006), and these likely reflect the differences seen in behavior necessary to ensure the survival of group members. By using this specificity in anti-predatory behavior, survivorship of group members can increase with increased fidelity and uniformity of the vocal signals used by group members.

One such paper examined the dynamics of snake detection (Etting et al., 2014). The authors noted that likelihood of snake detection increased as the test individual got closer to the study's snake model. Also, as long as one individual was close to the snake, the entire group could be able to understand that a threat is nearby. In this way, a single individual can share this information, though there is a risk to survival that comes with traveling in isolation. As only one discoverer is necessary for spreading this information to the entire group, traveling in groups is less necessary to the needs of survival as far as snakes are considered. This may prove different in cases regarding faster predators (raptors and felids). The authors also noted that when the snake model was covered so that the subjects could no longer see, the macaques exhibited more agitated behavior, as some tried to peer under the cloth and make sure that the snake had not escaped to another location. In the case of snakes, it seems likely that safety is increased given that the group present is aware of the snake and knows its whereabouts, whereas protection against raptors and felids may require strategies involving escape and higher density mobbing behaviors in order to increase the threat they present to the predator.

Contact Calls: Sociality Encouraging Safety

While these vocalizations are far less intimately associated with a predatory cost than alarm calls, contact calls represent an important way in which sociality, group cohesion, and cooperation ensure the survival of other group members. Through the use of these contact calls, macaques can know the whereabouts of another group member they are travelling with. In doing so, they ensure the safety of the other individual. It has been shown that the duration of the interval in between contact calls and their responses correlates with the distance between the individuals. In addition, when calls are not met with a response, the original caller will give another call (Sugira, 2007). The second attempt at a call is timed so that they only call when the interval has exceeded that the primate would expect based on their previous distance.

However, this is not the case for juveniles, who often break rules regarding waiting appropriately to hear a response and do not strictly adhere to turn-taking with regards to vocalizations (Lemasson et al., 2013). The transition from juvenile vocal behavior to adult behavior comes from learning the rules regarding these vocalizations. In learning the rules behind these vocalizations, this transition suggests that individuals become more cognizant of the response of others as well as the state of others, supporting the prosociality and cohesion of the group. Some researchers have considered this change in behavior to represent an emotional maturation, allowing for greater consideration of others' states after a period of social learning and development. Juveniles learn these techniques both through the rampant trial and response of their juvenile vocal behavior and by mimicking the rules used by the adults of their group. These adults may also reinforce this behavior, responding only

to vocal behaviors that are seen as appropriate, supporting the social cohesion of young.

Another important finding regarding contact calls regards the difference seen between the sexes in adults. While differences in female vocal behavior are influenced by age, male vocal behavior is influenced by dominance rank. Older females are more likely to coo call and contribute to informing other group members of her position, while low-ranking males demonstrate more vocalization than dominant group members. Given a matrilineal social society, the importance of older females' calls stresses the importance of these individuals within female cliques. They have stronger affiliations with the members of the group and have experience with coo calling. This experience allows them to mediate vocal interactions and enforce cohesion and safety in doing so.

With regards to the influence of dominance in male vocal behavior, given that male positions within the hierarchy are less stable than those of females, low-ranking males often call more often due to their lack of certain affiliations. In a few cases, it was noted that these males vocally behaved like juveniles, breaking turn-taking rules. Given the framework established in this thesis, I would predict that these juvenile behaviors seen in adult male Japanese macaques would not be seen in males of egalitarian species. As these males would have less behavioral anxiety regarding social organization and would be less likely to drift from the group, I predict that the organization seen in males would be more similar to that seen in females.

Conclusion

The game described at the beginning of this chapter fails to consider the many factors that contribute to altruism and social behavior, often resulting in strategies that would be undesirable in the wild. One such strategy I predicted in the game was that individuals would likely give to individuals of higher rank, as this would result in the greatest gain of Social Product. However, this is not true in the wild, as individuals are more likely to behave prosocially towards those with whom they have the most social ties, often resulting from kinship or similar rank. The value of these relationships and likelihoods must be considered in a broad framework. The players of this altruism board game may develop strategy based on the game's rules, but also result from the players' knowledge of one another. These players can use their knowledge of who's more competitive and who is more likely to cooperate and adjust their strategies to these needs. The resulting behaviors cannot be solely predicted by the cards drawn from the box. Similarly, the aforementioned studies cannot address the entire histories of macaques involved in social interactions. All that can be described are the behaviors seen within observation windows and what any statistical trends across these relationships demonstrate about the group's dynamics.

The behaviors seen here may present a wide, confounding spread of factors involved in prosociality; however, each behavior seen here can apply to a model in which the costs (both small and large) of social behaviors (both passively and actively benefitting others) are met with exceeding benefits. Grooming is an excellent example of this, in which tit for tat transactions define social organization and reflect a group's need for cohesion. Grooming has costs in both the energy it takes to groom

and in the time lost grooming that could have been used to forage. However, these behaviors create a social atmosphere in which groups are cohesive enough to have better foraging success than they would otherwise. The altruism of grooming results in the group's passive benefits of sociality in an ecological landscape of shared resources. This does not mean that feeding is not void of directed prosociality, as vocal and other signaling behaviors suggest that giving of information (though sometimes costly) allows for momentary group benefits that may translate into gains for the altruistic individual. Finally, the risks involved in social defenses of predation are great. Even though these predators are serious threats, individuals share this information with others in the group. Through mobbing, cooperation lessens the likelihood that harm will occur, and group cohesion provides a basis for this level of protection.

They also correspond well with behaviors that can be regarded in a framework of social maintenance and upheaval. As noted before, the behaviors mentioned in this chapter are those I primarily consider under the umbrella of "social maintenance" behaviors. Grooming behavior is the manifestation of social organization and hierarchy, as like individuals can groom like individuals in forming affiliations with other group members while also taking time and effort to groom unaffiliated members such that group members are more likely to behave cooperatively and less likely to leave the group cause the group harm. These reflect ecological needs of the group, often regarding foraging. By giving other group members information about food sources and allowing food to others, the group is maintained and hierarchies remain relatively stable, as valuable individuals

(regardless of how asymmetrical their rank is) tend to allow food resources to members of the group. Predatory threats present social maintenance in its most extreme form, as group members use their time and energy to ensure the survival of other group members. By ensuring the lives of these others, individual macaques uphold that the loss of another's life, even if they are unrelated, is something that can be a negative influence upon the group, as it would threaten preexisting relationships and interfere with the group's history of survival. While the onus of the terms "egalitarian" and "tolerant" reflect a top-down approach to social organization, this framework describes ways in which subordinates influence social dynamics. Through these behaviors, subordinates can manage their own success, by maintaining valuable relationships and optimally foraging (both socially and separately) in doing so. By conserving social order, these groups reflect an ecology in which most individuals do not treat the dominant individuals as dominant, but rather treat them as having high social value regardless of their affiliation. By forming affiliations with more like members, survival is more tangible, and behaviors that would result in one's gain in rank become less profitable options for individuals.

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Chapter II

The Play's the Thing

The behaviors many refer to as play pose an interesting predicament in understanding sociality of macaques and determining this behavior's roles in allowing for social maintenance through social cohesion while occasionally precluding aggression that may result in social reformation. While understanding what exactly makes such disparate paths possible in different social scenarios can be quite difficult when studying non-human primates, it may be of use to understand how play results in aggression in humans.

Consider a children's playground. In such an environment it seems likely that children will split up into groups of those who are affiliated with one another, often coming to the playground with these individuals. However, there will be times when they encounter others and may initiate play with those whom they do not know. Occasionally, there will be conflicts resulting from these interactions, as pushes (both accidental and purposeful) may occur, and wait times to go down the slide may begin to frustrate the playground's children. It is important to note that while children are the primary players in these scenarios, their watchful parents play an important role in the facilitation of play. If a conflict were to arise, these parents (and other guardians) will often intervene and attempt to lessen any damage the conflict has produced. Meanwhile, these watchful parents do not spend their time solely ensuring their children's safety. They may make small talk with one another, more often than not doing so with the parents of their child or children's friends. It's an important social activity for all involved.

Macaque play is an important behavior to note, as it establishes more subtle relationships that are founded on behaviors that do not have salient, immediate benefits. Play helps establish these relationships and is likely to perpetuate relationships within the sexes and within age groups. While such divisions of the group based on sex and age seem to contradict the implications of an egalitarian society, these biases in play ensure tolerance within these subgroups. For instance, by partaking in slightly rambunctious behaviors with those whom they trust, juvenile may develop a threshold for aggressive interactions so that extensive antagonistic relationships do not form. By allowing for social tolerance within these demographically determined subgroups, social maintenance can occur. However, this does not always occur, as play does sometimes lead to conflict.

Also, there are instances where play between the sexes and between adults and juveniles occurs, and it is important to address when and between whom these occur. While mother-infant relationships logically would result in behaviors some observers would describe as play, it is important to note the occasional behaviors that occur between adult males and juveniles. A common behavior seen involving both adult males and juveniles is bridging. Bridging behaviors are initiated when an adult carrying a juvenile offers it to another individual. The recipient will often accept this invitation and hold on to the juvenile as well, as both adults proceed to groom and/or lick the youngling.

The Altruism Game (Again)

When reconsidering the altruism game with the ambiguous and divergent effects of play in mind, it's easy to imagine the many paths players can take in order

to have as high a score as possible while also maintaining ample resources. While the game is established on sharing of resources, behaviors that would preclude social maintenance in a wild setting, the players respond to one another in ways that do not immediately and directly relate to the gameplay. They may audibly cheer their victories and groan at their losses. These demonstrations of their emotional state may be met with a response from their fellow players. In other words, though the game involves the mechanics regarding reciprocity, the way players respond to one another is very telling of how play functions in both human and non-human primate societies. Just like in the case of the card game's players, playful macaques respond to one another in ways that induce proximity and cohesion and allow others to better understand their behaviors.

Sex-Specific Affiliative Behavior and Rank Relations

When considering the play behaviors on the human playground, one often imagines boys and girls dividing accordingly into typically gender segregated groups of friends. This extends throughout all manifestations of their play, dictating not only whom they play with, but what they play with as well. There is even some evidence of this in non-human primates, as female juvenile primates often select toys differently than males. For instance, these females are more likely to pick a figure with a reddish face, possibly suggesting that they are more selective in finding a doll with a face that more accurately resembles a conspecific (Alexander, 2003). As a result, many studies on play focus on the relationships between members of the same sex.

Research on male Tonkean macaques has indicated the influence of greetings on their social interactions (DeMarco et al., 2014). I am considering these greetings play, as they involve both facial expressions unique to the behavior as well as some physical contact. It was found that, for Tonkean macaques, these play behaviors were not correlated with age and dominance status. In other words, these greeting behaviors did not appease relationships that are socio-ecologically strained such as those between dominants and subordinates. However, dominant individuals initiated approximately two-thirds of the greetings observed. It was also found that those who spent more time together tended to greet one another more often. Also, those who commonly greeted one another historically demonstrated few conflicts. This greeting behavior strengthened and maintained preexisting social relationships, supporting cohesion. It is important to note, also, that these greeting behaviors are not directed towards individuals with whom these macaques have had conflicts, suggesting a placating function. In these Tonkean macaques, it seems likely that the relationships that are most highly valued are those that are pre-existing and stable. Greetings between unaffiliated individuals aren't absent, but more costly play and interaction would likely occur in order to acquire and secure a new valuable relationship.

Given that the species involved is “egalitarian,” it begs the question of where else ritualized greetings occur. While they often occur in other tolerant species, these authors note that they are quite rare in rhesus and Japanese macaques. One behavior that sometimes occurs in these species is sexual mounting, in which high-ranking individuals are more often than not the individuals mounting the subordinate. Given the large hierarchical steepness in this species, it seems more likely that these

dominant individuals are essentially forcing relations with subordinates such that they can stay on top and maintain their position. Also, this mounting behavior may be a result of mating pressures that result in sexual activity between males.

In a study on an all-male group of Japanese macaques, researchers noted the occurrence of mounting behaviors and other acts that often are associated with these consortship events (Leca et al., 2014). Some of these inter-mount behaviors were grooming, feeding, resting, and huddling, all behaviors that are associated with male-female sexual bouts. This species contains groups that are relatively low in females, such that mating seasons are highly competitive. As a result, play becomes a more socio-sexual activity, demonstrating dominance over other individuals, regulating group tension, substituting for heterosexual sex when mates are unavailable, and potentially allowing younger males to practice for future sexual events. Given the similarity of behaviors associated with male-female and male-male sexual activity, it is difficult to determine the nature of these sexual acts. While it is possible that they can be substitutes for heterosexuality that cannot occur in an all-male society, they may also bolster the group's pre-existing relationships.

It is often difficult to separate social needs from sexual ones in these scenarios. While male-male social activity can be explicitly sexual in nature, it has been shown that male-male social affiliations enhance sexual and reproductive success for males. Conversely, for females, these social affiliations ensure the survival of offspring, but female social bonds do not suggest an increased likelihood of mating, as the number of sexually mature males in macaque groups almost always exceeds the number of receptive females. These female relationships are often based

on kinship, as social bonds that result in increased offspring survival may result from indirect selection. Thus, there are different mechanisms by which male and female play can lead to increased success and therefore are examples of costly cooperation that results in their own benefits through a rewarding social network.

I cannot overemphasize the importance of male's departure from their natal group in determining social development of male macaques. One study (Hassett et al., 2009, 2010) demonstrated that male rhesus monkeys approximately a year in age begin to socially segregate from the rest of the group, participating in both grooming and forms of play with individuals. However, females do not heavily bias their choice of playmates, choosing individuals in a rather random manner. Another thing that is important to note is that females would also associate and spend more time with older group members than males. As these developing males are likely not going to stay within their natal group, both the social relationships they have with their own age-group members and with adults are rather short-lived, whereas females are going to be around these females regardless and may as well reap any possible benefits from active participation in the social group. Also, though these male social groups are not going to last until they start mating, it seems likely that these male group formations are preparation for the male groups they will form with other immigrant males when they join a new group as adults, rendering these groups developmentally critical.

The types of play that females and males participate in are distinguishable. Males are more likely to engage in "rough-and-tumble" play than females. Young females, like the rhesus macaques that preferred playing with flesh-colored figures, were more likely to interact and play with infant monkeys than males. While it can be

argued that this behavior prepares young females for when they will care for their own offspring in the future, it is also important to note that these neonates may be valuable relationships as part of the group in the future. Males, who are only in the group for so much longer, don't have an incentive to care for neonates who will likely not reach an age at which they'd be eligible affiliates. Also, while the rough-and-tumble lifestyle that is unique to male macaques helps establish these segregated groups, they also may have an indirect relationship with the male's post-puberty emigration. As rough-and-tumble play likely establish rank and hierarchy and rank is a strong predictor of the age at which individuals will emigrate, the rough-and-tumble behaviors acts as a training ground for who is fit to leave first and assimilate into a different troop.

Both sexes demonstrated grooming and parallel play equally. Parallel play was defined as no contact, low energy play. A good example of this is social object play, in which two or more individuals handle an object, often taking turns between them (Yanagi and Berman, 2014, Shimada et al., 2006). Play-chasing is often involved, as individuals chase the object handler in order to acquire it. This is true regardless of the age, rank, and sex of the macaques involved. In general, it appears that this behavior is relatively void of effects based on sex. Though the researchers noted no effects of age on chase responses, the behavior is generally seen only in young macaques. While sex describes a number of behavioral differences, younger individuals often demonstrate general and short-lived behaviors such as these.

However, it is important to note that such object play behaviors, though primarily a juvenile phenomenon, are important for introducing novel behaviors.

Such object play would have been critical to the aforementioned root washing seen in some groups of Japanese macaques. Another novel behavior in Japanese macaques is dental flossing with thin strands of grass and twigs (Leca et al., 2010). By residing in socially cohesive groups and participating in social object play, it is more likely that adaptive, fitness-increasing uses for objects in the environment will arise and spread throughout the group. Also, certain non-adaptive, cultural styles of object use will often result, as one group's way of handling stones will be different than another's (Leca et al., 2010).

Age-Specific Affiliative Behavior and Rank Relations

Christine Reinhart's dissertation (Reinhart, 2008) on the juvenile behavior of macaques demonstrates the difference in play between egalitarian and despotic species. In looking at play behavior of young macaques in a despotic species (Japanese macaques) and an egalitarian species (Tonkean macaques), she acknowledged the extent to which their behavioral repertoire is similar, while the frequencies of certain actions help define their differences in a socioecological context. It was considered more aggressive when the macaques chose more vulnerable play targets on their playmate's body. For instance, biting hands and the head or face were considered more aggressive and less playful than biting the upper arm and neck region. Certain defensive responses were also considered more aggressive and indicative of more competitive play. While staying at the eye level of the other playmate and being vertical were common responses, biting was seen as an indicative of competitive defense while pushing oneself away in defense was seen as cooperative.

It was noted that Tonkean macaques tended to bite the more play-indicating, less vulnerable regions of the body, the neck, shoulder, and upper arm. Japanese macaques defensively bit more often than Tonkean macaques. The researches noted, however, that play behaviors seen in individuals were flexible depending on the demographic symmetry of the juvenile dyad. Levels of competition increased as the age difference and rank difference between the macaques increased. When considering the behaviors of similar pairings, it was found that Tonkean macaques tended to engage in longer play events than Japanese macaques.

However, Reinhart describes conditions under which Japanese macaque play tends to be longer than Tonkean macaques. As play behaviors can manage levels of group cohesion and ensure social maintenance, it seems logical that similar members of a more cohesive group would play longer than similar individuals of a less cohesive species. Tonkean macaques of similar rank play for relatively long periods as these reflect and maintain the networks of cohesion seen between group members. In the less cohesive, more upheaval-tending species, play between juveniles of different age and rank may be longer as playing longer allows the subordinate juvenile to either establish a valuable relationship with the dominant juvenile or defeat the dominant. While a playful “win” over a dominant member is unlikely, these may occur when Japanese macaques partake in more aggressive behaviors that, while risky, allow for playful victories over opponents that may influence the hierarchy amongst juvenile group members.

Reinhart also casually asks the question of whether the differences in juvenile behavior between these species can be demonstrated shortly after birth. In other

words, do the behavioral differences in juveniles across species reflect learning and social development or are these differences demonstrated from the outset of play behavior? In an attempt to answer this question, the author recalls a paper that demonstrates that dominance behavior can be demonstrated in the first few weeks of life (Norikoshi, 1974). This is a rather genetically deterministic view of social behavior, suggesting that behavioral strategies and tendencies that are different at the moment of birth.

However, if these behavioral tendencies are established from birth, this calls into question the plasticity of behavior seen in the different aforementioned contexts. This deterministic view suggests that infants understand their rank at the moment of birth, whereas rank can be moderately flexible, especially in more despotic species. I suggest, instead, that the early instances of rank-related behavior mentioned in Norikoshi's study are not representative of behavioral genetics, but indicate the tremendous impact of maternal rank on early behavior formation. In order to test this hypothesis, I suggest that future studies could demonstrate whether juvenile rank and rank-related behavior more closely resemble that of the mother (providing both genetic and environmental contributions) or the father (providing solely a genetic contribution). While studies of the behaviors of orphaned macaques raised by humans may prove useful, it seems possible that these infants would learn from the humans that feed and shelter them. Also, the number of additional factors that would contribute to their social differences would not provide for an adequate setting for comparative observation.

Maternal-infant behaviors seen in these first few weeks of life indicate the importance of imitation in behavioral learning. Studies have shown the importance of certain critical windows, as infant rhesus macaques begin to imitate their mother's lip-smacking behavior and tongue protrusion at three days of age (Ferrari et al., 2006). While these behaviors in such young individuals do not compare easily to the affiliative interactions seen amongst older juveniles, they indicate the importance of imitating other primates in play and other social interactions and how behaviors can be learned via imitation at a very early stage in primate development. Also, it must be noted that while a number of primate facial expressions can be considered prototypical, being common across all populations of a species or even a genus, there are a number of facial signals and other social gestures that are specific to groups and vary across populations.

These facial signals are also in cultural flux, as different play faces can originate and transmit across group members (Emory et al., 1979). Some researchers have even suggested that vocal signals can be substituted for play faces given the absence of face-to-face contact, as is sometimes the case in wrestling play (Kipper, 2002). This suggests that different modes for transmitting information are possible and present and that these signals may vary depending on populations, their social development as juveniles, and the resulting play behaviors they typically engage in.

Also, given these differences across primate populations and how these behaviors seem parallel to the variety of social gestures seen across human populations and cultures, it seems likely that certain behavioral differences are the product of memetics, not genetics. Memetics refers to the transmission and

replication of units of culture (Dawkins, 2006); in this case they are behavioral signals that provide social information. These would be difficult to transmit across groups, though the signals themselves do not indicate differences between groups. It simply demonstrates geographical separation that has allowed for different cultural ideas to repeat themselves and become stereotyped over time.

All in all, these differences support the notion that social behaviors and signals have extensive socio-ecological and learning components. It also seems likely that play functions similarly given the diversity seen. However, given this knowledge about the diversity of facial expressions across primate groups or even within certain play pairings. It could be that certain novel play behaviors may exist in different groups of macaques. These behaviors would not indicate that this group is somehow qualitatively different than another; they would only suggest that these behaviors were founded by a member or members of the group and were ritualized over time through the group's social interaction.

Play, Age, and Long-Term Sociality

Studies on adult play have shown that the development of play differs between species of macaque. One such study compared the play behaviors of Tonkean and Japanese macaques (Ciani et al., 2012). This study demonstrated that egalitarian-type species retain some juvenile characteristics of their play into adulthood. Firstly, it is important to note that, even as juveniles, Japanese macaques played less than Tonkean macaques. While some of this difference may be attributed to the juveniles themselves, this could be related to the trend that their mothers are less likely to be social, putting them at a distance from potential playmates. These low

levels of playing may then follow them into adulthood. Also, it was found that adult Japanese macaques preferred playing with young group members while Tonkean macaques showed no such preference. The authors attribute this to female behavior, as there was a significant difference in levels of play between females of the two species but not a significant difference between males. In these cases, it appears that females regulate the dynamics of play seen in the group, as Japanese macaque females both inhibit the likelihood of their offspring finding a playmate.

Another study on crested and Japanese macaques (Petit et al., 2008) found a similar trend, as Japanese macaques were less likely to participate in riskier play. They were less likely to make physical contact and tended to participate in adult play activities with fewer members, such that escape was easier. It would appear from these behaviors that there is more risk of aggression in such play events, whereas the threshold for rambunctious activity is lower in crested macaques. It could be possible that the differences seen in play behaviors are regulated due to the sex ratio and spatial relationships of these populations. As “egalitarian” groups typically have a higher male:female ratio, they have less male-male competitive pressures and are more likely to be in proximity with one another (Singh et al., 2009). This enforces a structure in which one another’s presence is tolerated and, therefore, some levels of aggression are considered non-threatening and can even be used to further social cohesion via play.

Interestingly, some authors (Ciani et al., 2012) have compared the differences in play and parental care seen in these macaques to the differences seen across human groups as noted in anthropological literature. In this analogy, Japanese macaques are

more like agricultural societies, in which there is a hierarchy of who has what job on the farm. This dynamic enforces differences between sexes and ages. Tonkean macaques are more like hunter-gatherer societies, in which populations are mobile in many senses of the word. It has been noted that hunter-gatherer children are found playing without parental care, often doing so without bias towards kin or their own age group. In these groups, alloparenting is far more likely and encouraged, whereas farm life often results in spatial separations based on kinship.

These comparisons ask the question of whether these differences can be ascribed to genetics or culture. In the case of humans, this variation falls under a single species whereas, in *Macaca*, these differences provide further justification for taxonomic differences. However, seeing as how these behavioral differences can result from a social ecology or environment demonstrates the power of social environment in influencing behavior and its evolution and development. The authors state that this may be a case of self-domestication, in which the group dynamics select against aggressive behaviors and for prosocial behaviors. In an environment where behavioral selection is directly acted upon by the group, could it be possible to describe this process as artificial selection? It may be revealing to reflect both upon human behavior and history in order to understand the behaviors of these macaques. As certain environmental conditions precede the formation of nepotistic farming societies, these environments may suggest the influences that would precede nepotistic behaviors in macaques and how these may influence the sex-dependent sociality in these species.

Adult-Juvenile Interactions

As noted before, the majority of play behaviors are dependant on age and sex. However, behaviors between adults and infants are also common. Beyond the relationships seen between mothers and their children, it has been shown that other adult females will form relationships with these infant macaques (Ogawa, 2006). While many of these individuals may be sisters of the mother or other forms of kin, interactions between non-kin and infants suggest the role of affiliative networks. By playing with these infants, adult females strengthen the relationships they have with their mothers. In some primate species, the relationships between adult females and infants begin as early as birth. Recent studies in white-headed langurs have shown that other females will help during the process of birth (Pan et al., 2014). In this species, it was found that these helpful females would help remove the infants from the birth canal and cared for the infants while the new mother recovered. While this observation has not previously been described, it seems possible that such behavior is not uncommon in primate species, as many birth events occur at night and have not been observed in the field. By helping other mothers, females can increase their inclusive fitness and strengthen bonds. A common adage states that it takes a village to raise a child, and it seems like this is no less true for non-human primates.

One complex behavior involving infants has attracted the interest of many researchers. This behavior, called bridging, involves two adult members of a species and an infant. The individual carrying the infant gestures it towards another adult, signaling desire to commence bridging. In accepting this initiation, the recipient grabs onto the infant as well. The two adults occasionally vocalize, groom the infants fur,

often licking the genitals of the infant. This behavior raises the following question: what value do these infants' have to these adults and what does the relationship between the involved adults suggests about the origins of this behavior?

Also, this behavior is seen extensively in male individuals, who would not know whether they are genetically related to these infants and, based on semi-random chance, would not likely be. A number of hypotheses regarding adult male-infant have been used to explain the presence of male-infant behavior (Bauer et al., 2014). The first of these hypotheses suggested that adult males, by performing these interactions, increase the fitness of infants who may be their own offspring. However, no mechanisms have been described that would allow adult males to discriminate offspring from non-offspring. Also, it has been demonstrated in the wild that males are no more likely to initiate bridging with their own offspring. A second hypothesis suggested that males play with young group members in order to increase their access to mates. Females who witness these caring behaviors would see these behaviors as desirable and would be more likely to mate with them. This hypothesis has received less support.

The most well supported hypothesis suggests that interchanges between adult males and juveniles result in strengthened affiliations between male members of the group. Also, this effect would be hard to discriminate from an effect on female mate choice, as individuals with social bonds tend to be more reproductively successful (Schulke et al., 2010). However, if this is to be true and the infants are merely tools for reinforcing and strengthening male social organization, then infant choice would be indiscriminate. However, this is not what is than female infants. Does this suggest

that these males are initiating these juveniles into their social group? In all likelihood, these males will leave their natal group after puberty; however, some males do stay. Are male infants who regularly are used in bridging more likely to stay in their natal groups?

Female Social Organization and Adult-Juvenile Behavior

Before exploring the behaviors of males and questioning these hypotheses, it is important to address female behaviors regarding juveniles in order to compare these sexes. Bridging has been observed between females in rather different contexts, as these females are often the mothers of bridging infants involved. Female Tibetan macaques have been known to initiate bridging behaviors with other recent mothers (Ogawa et al., 2006). It seems possible that these gestures are affirmations of alloparenting, as two recent mothers doing so suggests that they will carry, protect, and socialize with the other's infant. In other cases, it is difficult for other females to approach a new infant. In order to approach the infant and mother, these females have to gain trust through prosocial behaviors.

A study regarding infant handling by females revealed a number of trends, suggesting reasons behind females' carrying of non-kin infants. While some have suggested that handling another infant results in increased infant survival, as such handling allows non-mothering females to gain experience, this was not demonstrated. Infants of common handlers were no less likely to survive than inexperienced mothers. One interesting observation was that infants were often handled by mothers who had lost their own offspring. In doing so, these mothers may be reducing stress resulting from these events. Also, those who did not have infants

were more likely to carry, suggesting that raising offspring is costly such that helping other mothers would not be possible or adaptive. Though bridging does occur between female mothers, the vast majority of non-maternal, infant-directed behaviors are from female adults without infants. Some have suggested that carrying infants is actually a selfish behavior, as doing so actually decreases the success of the infants involved. However, it has been not shown to be a harmful behavior.

The most common explanation regards kin selection, as those who are genetically related to these offspring would have reason to invest in carrying and protecting these infants. However, this would not explain those behaviors seen where non-kin carry these infants. Another hypothesis suggests that carrying is simply a byproduct of maternal investment evolution. As mothers have evolved to invest a lot in their offspring, these behaviors have become somewhat general such that adult females will care for unrelated offspring. This would explain why those without their own offspring are likely to do this. Carrying infants may be the norm for female macaque behavior. While mothers can easily appease this need, non-mothers will occasionally use other's offspring. However, this calls into question infant choice. While one article I will describe later delves into infant choice on the part of males, I have yet to find a study that directly addresses adult female's infant choice.

Male-Infant Behaviors: A Case for Male Social Cohesion

While triadic interactions make the social benefits of male-infant interactions apparent, one study has shown that carrying infants is associated with more access to male social networks. In addition to this access, it was also demonstrated that stress levels are involved in these male-infant behaviors. While these behaviors receive

benefits from this access, male infant carriers had significantly higher levels of glucocorticoids than non-carrier males. The authors in this paper suggest that this indicates that carrying infants is a highly costly behavior that is outweighed by the benefits received from having access to social networks (Henkel et al., 2010). However, this again raises the question of how stress would influence infant choice. It seems possible that certain infants would be more stress-inducing than others, as these infants may cry more or be more physically demanding on the carrier, as older juveniles are sometimes carried as well. The researchers in this study also doubt the possibility that individuals who have more stress are more likely to carry infants. However, since these individuals who carry are doing so in order to gain access (and especially during times of inter-male tension), it seems possible that doing so would result in decreased stress. While non-invasive fecal studies demonstrate high levels of stress hormone individuals, it would not be possible to see if these drop in a single bout. While the researchers note that there are no longitudinal decreases in stress, this does not suggest that carrying an infant can provide short-term endocrine relief in addition to the aforementioned social benefits. In order to do so, it seems like an experiment in which heart rate is recorded before, during, and after infant carrying would suggest any immediate effects on stress.

Paul et al. (1996) tested the three aforementioned hypotheses regarding male-infant sociobiology. Using DNA fingerprinting, paternity could be determined in the Barbary macaques of this study. After observing several bridging behaviors, it was determined that kin were not more likely to be chosen. The mating effort hypothesis did not receive support, as the males involved in bridging were not more likely to sire

the next infant of the mother of the infant used in bridging. However, this is a reduced version of the mating effort hypothesis, as it does not demonstrate whether those who are involved in bridging are more likely to sire an infant, regardless of mother. However, such an inclusive definition of the mating effort hypothesis would be difficult to delineate, as rank effects could be significant contributing factors. Also, as noted before, it is difficult to determine how bridging infant choice is determined. Given that popular infants are not always the highest in rank, it could be that there is a trade off between choosing an infant from a valuable mother and choosing a less risky infant that will less likely result in maternal aggression based on rank. If this is so, then it seems possible that males who care for infants are doing so to impress high-ranking females who are not the mother of the infant.

In this study, a number of nuances to the agonistic buffering hypothesis were noted. First, triadic interactions between two males and an infant (like bridging) were shown to often include at least one member of high rank and often occurred between male individuals who were similar in rank. In a few cases, grooming followed the triadic interaction, with the individual of higher rank being the primary recipient of grooming. Another critical observation was that these triadic interactions were observed more often during periods where inter-male interactions were typically aggressive. This suggests that these behaviors establish and support affiliations between these males. The question remains: why involve these infants?

Bauer et al. (2014) tried to address this question by researching the factors that influence choice of infant bridge partners. It was found that, for this group of Tibetan macaques males were preferred over female partners. One male individual was used

most often in these interactions, as every adult male was observed in a triadic interaction with this infant. However, no relationships could be seen between these infants and adult male-female interactions. The infants chosen in these interactions were not shown to be the offspring of females that were affiliated with the carrying male(s). As a result, the authors offer a suggestion as to why this is so. They suggest that infant choice is a result of the agonistic buffering hypothesis. Because this behavior has been shown to support affiliations between males and allow access to networks with individuals of higher rank, the authors suggested that certain infants would be particularly popular because the highest-ranking male(s) prefer to bridge with this infant. While this does not explain why males would prefer these infants, it does demonstrate a reasonable solution to the question of why infants are so popular. This does not suggest that this infant male was more available for adults to use for bridging, as this individual was often chosen even when other infants were in close proximity. Also, it has been found that these infants are preferably chosen in instances of carrying as well, as males will more often initiate bridging with infants they typically carry.

Play, Sociality, and Conflict

While it has previously been established that play can be oftentimes competitive, resulting in increased likelihood of aggressive, potentially injurious behaviors. However, play can sometimes have a mediating role in conflict. For instance, if two individuals are behaving aggressively, a third may come in between the aggressive individuals and initiate less aggressive play. Conversely, an interesting

phenomenon has been noted in which individuals adjacent to a conflict are more likely to behave prosocially towards nearby affiliates.

Observations in Tonkean macaques have demonstrated the phenomenon of peaceful interventions during times of conflict (Petit and Thierry, 1994). In fact, these playful distractions were twice as likely to end a conflict when compared to aggressive intervention behaviors. As it has been demonstrated that most conflicts occur between males, males intervened more often than females. Peaceful intervention was especially potent as the intervening individual was almost always of higher rank than those involved in the conflict.

This was not the case for aggressive intervention. Two factors increased the likelihood of intervention: relations between the members of the conflict and nearby, potential interveners and the severity of the aggression seen in the conflict. Interveners were more likely to do so peacefully when their kin were involved in the conflict. In these cases, the intervener will usually target their non-kin aggressor in order to cease aggression. Some common intervention behaviors are clasping behaviors, playful nibbling, lipsmacking, and other gestures that will remove the aggressor's attention from their kin or close affiliate. The dominant intervener doubly receives benefits from this costly interaction. First, the action protects their closely related kin or affiliate; second, the interaction between the intervener and the aggressor establishes a relationship between these members, ensuring a more respected dominance and potentially decreasing the likelihood of future conflicts. The latter is especially likely, as the intervention period often extends into post-conflict grooming.

In the study regarding affiliative behaviors on the part of conflict bystanders, it was found that these individuals often behaved prosocially after the nearby conflict had ceased (DeMarco et al., 2014). These individuals are not directly affected by the conflict, as they were not being aggressed upon and were not in danger of being. This suggests that a post-conflict environment creates social tension such that nearby individuals compensate by behaving more prosocially than they would normally. In some instances, signs of anxiety such as the self-scratching behaviors mentioned in the previous chapter were noted. In doing so, the presence of these anxiety-suggesting behaviors is reduced and social cohesion is maintained despite the brief tension. This would explain why females are quicker to respond prosocially than males, as their social networks are larger and have a longer history. Another thing to note is that these behaviors were not directed towards kin, preferring those who are closely affiliated but not kin. This may suggest that kin relationships are more persistent and less vulnerable; therefore, more effort should be directed towards non-kin in order to preserve these relationships during periods of social tension.

While the authors of this paper noted that social affiliates were more likely to behave prosocially towards one another in this post-conflict environment, they did not elucidate whether certain individuals were more affected by the conflict they were near to. For instance, do close affiliates and kin of the conflicting individuals show a greater prosocial response than those who have fewer social ties? If this is so, it seems that there are a number of conflicts of interest that may play out in the event of conflict. First, during the conflict, individuals may be inclined to behave in a risky way and intervene. However, there is also a possible component of stress that may

impede the individual's will to end the conflict and, rather, reduce this social tension by interacting with nearby group members. Also, in the event of successful interventions such as those noted before, it may be shown that there is a decreased response from bystanders, as the conflict has been effectively reduced along with the social tension of the environment.

Conflicts may pose threats to the cohesion of a social system, but it seems possible that these routine maintenance events not only secure these social bonds but establish new affiliations as well. In this way, play can be seen as the centerpiece for establishing the social environment in which maintenance behaviors and upheaval can occur. It allows for individuals to test the boundaries of the individuals around them and determine routes to success within the group and how to achieve the greatest success without taking too much risk.

Conclusion

As evidenced by these articles, play behaviors hold an ambiguous position with regards to understanding the sources of prosocial behaviors. Play is not necessarily a prosocial behavior, as play itself can be aggressive. However, is this aggression something that is necessarily unhealthy to the group? Given that these instances of aggression are rarely dangerous, could it be that play, both peaceful and aggressive, strengthens social relationships within the group. By allowing for methods of reconciliation, it could be that social relationships emerge stronger than they were previously after these aggressive bouts.

Consider human relationships. There are certainly some friendships I value highly despite the occasional stress they cause me. Sometimes this holds true to the

point where these petty grudges allow me to reconsider the value of this relationship and, in doing so, find more value in the friendship. This could also be a phenomenon in non-human societies. Through these periods of reconciliation, pairs are able to end on good notes, so that relationships are not severed. It would be of interest to see if these periods of reconciliation extend longitudinally, such that those who had an aggressive play fight will remain in closer proximity in the weeks (if not months) following these events.

In sum, the behaviors mentioned in this chapter demonstrate play's ability to facilitate social cohesion that allows for the behaviors mentioned in the first chapter. By spending time with other individuals, bonds are formed that preclude gifts like grooming. By sharing resources like food, time, and space, there are unwritten bonds between group members that need to be upheld regularly. Play allows for these behaviors to be upheld. While the previous behaviors involve the transfer of resources, play does not have an immediate benefit to the individual (except for neuroendocrine rewards). However, by forming socially cohesive groups, benefits like those seen in the previous chapter are more likely. By being in a group and miming the behaviors of others, macaque species make informed, collective, beneficial decisions that reflect the behavior of the group as well as that of individuals (Sueur and Petit, 2008; Sueur et al., 2009). Through the facilitation of cooperative play behaviors, individuals are more likely to behave in a collective, cooperative manner when foraging for food, when energy and time investments are higher.

Given these examples, play can be seen as a behavior that mediates social cohesion and occasionally results in conflict or is used to reconcile after such a

conflict. This calls into question the role of conflict within the groups. While group members can be severely ostracized by a cohesive majority, there is cooperation to an extent in this conflict. Even instances of behaviors that would be perceived as immoral or hostile in humans reflect a history of prosociality. If two males were behaving aggressively towards one another, one's friend might intervene in this once playful activity. By tipping this balance, the two may be far more able to harm this individual, reinforcing their separation from the group's core membership. It is important to realize that conflict does not exist in a vacuum where harming others is typical of the individuals involved, the group involved, or the species involved. Response to conflict operates on similar principles to those that governed the behaviors of the first chapter, and is mediated by a social environment enforced by play. In the following chapter, I will address conflict, intervention, and coalition-forming using the framework set in the previous chapters. In doing so, I hope to acknowledge the roles of cooperation and biased prosocial tendencies in mediating the antagonistic interactions commonly seen in non-human primates.

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Chapter III

Coalitions and Cooperation: An “I” in “Team?”

The Altruism Game Returns

As noted before, there would likely be a number of conflicts resulting from playing the Altruism Game. Some players may find it unfair that certain individuals have such control over resources and are able to accrue a lot of social value. As a result, like minded players who initially drew cards with lower rank may work together in order to perform better across their ten turns, coordinating their choices in order to increase in rank, receive adequate resources, and, potentially, lower the rank of a targeted despot. This can be seen in macaque societies of high hierarchical steepness, in which subordinate males are better off working together in order to have control over the spaces they occupy and challenge the control of the highest ranking male or males. However, this is not always the case. Despite the peaceful connotations of the label egalitarian, members of these groups are more likely to direct their coalitionary antagonisms towards recent, unassimilated immigrants (Berghänel et al., 2010). These groups may show high ingroup cohesion and low ingroup competition, resulting in egalitarian characteristics, but these groups, being social maintainers, are resistant to change that could be imposed by newly arriving males.

The concept of intervention can also be tackled in this game. Though some group members may work together to better compete with the highest ranking player, some players may not direct such antagonism, remaining neutral despite the situation. This behavior is certainly not uncommon in the primate world either, as some group

members do not commonly participate in group or solo antagonistic interactions. While it would be hard for a human player to intervene in the profound ways demonstrated by macaque behavior, their cooperative interactions with conflicted players may alleviate some of the game's tension. By doing so, they are inhibiting the player or players' attempts at a rank reversal. Conversely, if two or more players attempt to oust a struggling player by forcing them to forfeit the game, another player may intervene. This player's intervention may be based on the history between these players. A history of reciprocity may have led the player to behave prosocially and save the other player from a forced forfeit.

All in all, a number of factors can be seen here. First, there are factors stemming from the social histories between the members of the group; second, there are benefits and costs that come with working in groups. While it can be easily demonstrated that two individuals working together may have a better chance of defeating a dominant individual, this is not a foolproof method for success. There is a level of choosiness to coalition formation, and it tends to reflect both histories of affiliation and competitive ability.

Consider a game of unequal dice. Subordinate members each have a single six-sided die with the numbers 1 through 6. Dominant individuals have a die with the numbers 5 through 10 marked on its sides. If these two individuals were to compete, there would be only one instance out of thirty-six possible combinations in which the subordinate would defeat the dominant: when the subordinate rolls a 6 and the dominant rolls a 5. However, if two subordinates were to challenge the dominant individual to the same game, combining their scores in order to trump the dominant

individual, the odds of success increase to 37.5%. In this dice-rolling model of coalition-formation against dominant individuals, one can reduce the rank steepness by lowering the values on the dominant's die. By lowering the dominant's die to values from 4 to 9, the odds of success for two individuals in a coalition increase again to 50%.

However, these odds of success would dramatically decrease if the dominant individual was also able to recruit other individuals into such an antagonistic interaction, reducing the subordinate comparative ability. In this way, coalition formation is a battle of costs and benefits that may be very difficult to determine and are highly dependent on the group dynamics governed by social history and ecology and the needs and histories of the individuals involved. For instance, a highly subservient subordinate may form a coalition with the dominant individual. However, in a more skewed group of macaques, the dominant individual may have fewer potential allies, and the likelihood that coalitions will be able to recruit like members against a dominant individual or smaller group of dominants is much higher.

Given that the members of a coalition each have the ability to receive gains from a successful bout, it is difficult to refer to this behavior under an altruistic framework, in which there would be significant costs for one individual in order to better another individual. However, if the comparative benefits and costs for the individuals that unite in these coalitions differ greatly, coalition-formation could potentially be considered altruism, in which one individual incurs cost in order to help another benefit. This may be the case in instances where higher-ranking individuals unite with lower-ranking members. The lower-ranking individual may receive more

benefits from this interaction, such that the higher-ranking individual receives only longitudinal benefits through the increased value of their relationship. Some have given names to these different types of coalitions. Those in which the both coalition members are stronger than the target are considered all-down, while coalitions where both are weaker are considered all-up. Those in which only one individual is stronger than the target are considered bridging (Bissonette et al., 2009). Given this asymmetry between the pair, it could be said that this is an altruistic benefitting of the weaker individual while the higher-ranking helper incurs a cost.

Additive Ability and Coalition Formation

Bissonette et al. (2009) attempted to mathematically quantify the odds of success for coalitionary behaviors based on the overall additive strength and ability of the coalition's members compared to that of the target. Overall, it was found that coalitions of Barbary macaques are generally successful with a rate of 72.2%. This rejects a null hypothesis that two heads are always better than one, as a number of these coalitions were not successful. In order to better understand why successes and failures occurred, these researchers quantified the difference in strength between coalitions and targets. They found that greater differences in the competitive ability of coalitions and targets resulted in increased success rates, whereas slimmer differences were less certain successes. Approximately 78% of the variation in success rate was attributed to the quantified difference in competitive ability.

In Barbary macaques, it has been found that their coalitions tend to be all-up, directed towards higher-ranking individuals. The researchers involved in this study

were also interested to see whether these males were able to recognize the presence of asymmetry between coalition and target strength, as target males may respond differently when there is a stronger asymmetry present. This was found to be the case, as targets were more likely to counterattack against coalitions that were of lower competitive ability. If asymmetry was great, the target was more likely to simply flee. While this may suggest that these macaques are able to recognize a coalition's ability, the authors of this paper suggested that the target's response is solely based on the number of individuals in the coalition of higher rank. For instance, 78% of all-up coalitions were met with counter-aggression, while intermediate amounts of counter-aggression were observed against bridging coalitions, and no counterattacks were found against all-down coalitions. In this way, the target may only be recognizing the risk imposed by the presence or absence of higher-ranking individuals. In order to test this hypothesis, I suggest that future work on coalitions should use one-on-one aggressions as a means for comparison. For instance, if future studies find that males are more likely to counterattack when facing a single higher-ranking male than when faced with a bridging coalition, it would be suggested that the subordinate individual has an effect on the interaction. However, this study's data do not confirm effects of the subordinate.

Conversely, if it were to be found that the subordinate member of a bridging coalition has no effect on the behavior of the target, this would further suggest that bridging coalitions are an act of social altruism or, at least, that subordinates are utilizing their valuable relationships in order to receive protection from higher-ranking, stronger males. Again, in order to determine whether these behaviors are

costly, it would be interesting to better analyze aggression by targets. If these individuals tend to target the subordinate male, this could suggest that they perceive this male as being an easier fight. However, if the targets direct their aggression towards the higher-ranking male, it could be because this individual is perceived as being the more threatening figure in this context.

From the perspective of the coalition formers, it was also found that all-up coalitions are more likely to form given high asymmetry with their potential target. In other words, coalitions are more highly asymmetrical than would be found in models based on chance. Also, the competitive ability suggested by this model of coalition strength only relates to the odds that a coalition will win, suggesting that ability is determined by physical strength and rank. As macaque groups contain familiar group members, there are a number of social histories that play a part in choosing a partner, choosing a target, and carrying out an antagonistic behavior. The higher-ranking male may simply back down in order to avoid having an unnecessary fight in order to avoid reducing the social cohesion of a group. In order to test this hypothesis, one would need to look at all-up coalitions found in groups of less cohesive macaques (rhesus or Japanese). However, it would be difficult to determine whether these high-ranking individuals are more likely to fight for any given competitive asymmetry, as contributing factors are specific to the socio-ecological dynamics of the group at hand.

Mating Tendencies and Coalitions

Regardless of the species of macaque, it has generally been found that coalition formation is more common during mating seasons. This seasonal time of

stress and competition for males often leads to these combative moments between group members. As a result, some have looked at coalition formation through the framework of sexual competition. One study (Berghänel et al., 2010), again on Barbary macaques, followed hypotheses that scramble competition for mates would govern the dynamics seen in coalition formation. While models would suggest that Barbary macaque coalitions would primarily be focused towards high-ranking targets, this was not observed in this study. Instead, as a result of scramble competition, the males of this group targeted recent immigrant males in order to reduce the number of potential male mates and increase the likelihood of mating with one of the group's females.

In scramble competition, decreasing the effective group male number is a sure way to skew the likelihood of mating and passing on one's genes. Scramble competition suggests limited effects of rank, in contrast with contest competition, in which males compete with one another for specific female access. Given a moderate group of viable females and a smaller number of males, it is not a matter of who gets to mate with whom, but rather, who mates at all. Immigrant males disturb this and have no socially cohesive ties that would grant them access; therefore, they are excluded. This does not suggest that there is no contest competition, as females choose their mates based on their dominance rank. However, this merely results in exclusion of lower-ranking males in favor of any high-ranking males.

Given this mating landscape, these males behaved differently than those of the same species in the aforementioned study. Some characteristics involved in this design must be taken into account. First off, the study that primarily found immigrant

targets was done in a semicaptive environment for which there were no means for male dispersal to a nearby group. Whereas in one study of wild populations (Menard and Vallet, 1993), such immigrant males that are victims of antagonism may continue searching for a group that has low enough a male group size that an addition would not threaten the mating season. In this way, the dynamics of aggression observed within this species are quite plastic. Earlier models predict that larger male group sizes would be correlated with greater frequencies of coalition formation. Also, a similar study on wild Assamese macaques (Ostner et al., 2008) noted that highly targeted males often left their groups after receiving continued antagonism. While in the Barbary macaque study, targeting immigrant males kept them on the fringes of their focal group, this wild behavior suggests an intention of causing further immigration. However, this semicaptive environment does not allow for these behaviors. In another semi-free ranging study in Barbary macaques, however, it was noted that subordinate individuals primarily targeted prime, dominant males, suggesting that they may do so in order to receive mate access (Bissonette et al., 2011). It appears that behavioral variation exists across these populations, as sex ratios and resources vary.

Another thing to note is that these behaviors did not directly reduce mating opportunities for these immigrants, as the number of mating opportunities they had did not differ from mathematically expected chances for group members that spend most of their time on the outskirts. They were not as successfully excluded as would have been possible in the wild. By behaving aggressively, it seems that these social maintainer species are able to maintain group size and avoid the effects of additional

male membership on mating opportunities. In order to better demonstrate the diversity of coalition formation, it would be worthwhile to examine the behavior of groups that are particularly low in their membership and see how they respond to newly immigrating males.

Dominance Turnover

In addition to defining coalition formations by their membership, they can also be defined by their effects. Some coalition antagonism can be defined as rank-changing, whereas other instances can have no effect on rank. While studies have not noted these in a systematic way, anecdotal case studies have provided interesting details on their existence. Some have described these coalitions as being revolutionary, as their intended function seems to be reducing the dominance rank of the high-ranking target. In one reported instance of dominance turnover between an alpha (GN) and beta male (R7) Japanese macaque, it was found that drastic behavioral changes resulted (Kutsukake et al., 2005). After the turnover event, the beta male continued to behave aggressively toward the once-alpha male, asserting his new position as the highest-ranking male in the group. Oddly enough, this did not mean that the now-subordinate male reciprocated this aggression. In fact, it was found that GN often solicited R7 for aid and that R7 often reciprocated. In this way, R7 maintained this relationship, but now was the alpha male and occasionally antagonized his affiliate in order to maintain his new position. Also, in this period of instability, it was found that subordinate males were more likely to engage in aggressive actions towards dominant males, often doing so in polyadic coalitions.

These aggressive behaviors on the part of subordinates were not violent and ultimately ceased upon the re-stabilization of affiliations between dominant males.

However, some of the more interesting effects were observed in females. Following this turnover event, females severed their relationships with the once alpha male and, in some instances, mated with the newly alpha male, R7. It was also observed that six females became receptive at the time of the turnover. It was also observed that the alpha female and her daughters were the individuals who most often groomed and affiliated with GN after his removal from the alpha position. Again, this suggests that the group's behavior was performed in order to keep this member in their group, so as not to remove their valuable social ties while reaping the benefits of a new upheaval. These benefits may include changes in the genetic composition of future generations. Groups that frequently change their alpha males result in fewer paternally-related offspring across successive generations, increasing the genetic diversity of the group. For less despotic species, this is not necessary as males have less skewed access to available females.

While this event is rare and has not often been seen in the literature, its profound effects are very telling of the social organization of this group of macaques and how it reflects the needs of subordinates as well as lower-ranking dominants for change in order to have more control over resources, primarily food, mating partners, and space in which to control feeding and consortship behaviors.

Coalitions of Kin

It was demonstrated in Barbary macaque males that coalitions are twice as likely to form in support of kin than non-kin (Widdig et al., 2000). It has also been

demonstrated that, due to the more fluid nature of male social organization, there is a greater tendency to aid kin in females than there is in males. In fact, some have suggested a threshold for the effects of kinship in female social behavior. This aunt-niece threshold has demonstrated marked differences between the relationships of these close relatives and non-kin. Therefore, it would seem likely that reciprocity and selfish motives for coalition formation are more likely to influence the behavior of males. It was also noted in this population of male Barbary macaques that rank-changing, revolutionary coalitions are a relatively rare phenomenon, suggesting that coalitionary behaviors in this species are less driven by pressures to oust individuals.

One paper addressed the role of kinship in determining the coalition behavior of juvenile Japanese macaques (Schino et al., 2007). In this study, it was found that kinship was a good predictor of the agonistic support received by juveniles, though juveniles themselves were less biased towards agonistically supporting kin. These young individuals were shown to behave aggressively towards other juveniles whose mothers were relatively subordinate to their own, while they typically did not do so for dominant juveniles. The authors of this paper conclude that the juvenile behaviors seen here may not have been altruistic, as the refined knowledge of rank in determining juvenile coalitionary behaviors indicate a tendency towards isolating the weak while avoiding conflicts with those who are prospective dominants. This also suggests that, due to their lack of kinship bias, juveniles are better able to discriminate the rank of other group members than they are able to discern kinship. This suggests a rather anti-altruistic view of the species, such that kin support is secondary to competitive understanding of social hierarchy. However, an understanding of social

hierarchy may result in altruism later in life. By understanding who is dominant and who is subordinate, individuals may learn with whom to share valuable relationships and occasionally behave altruistically towards. Also, while these initial tendencies may be rather harsh towards subordinates, the development of tendencies for kin care and support may only be a result of the evidence that juveniles are not likely to be able to rear young. Therefore, development of kin-directed behavioral tendencies may be delayed, not because selfish rank concerns are the initial trait, but because rank concerns are more relevant to the social landscape of juveniles than kinship.

Coalitions of Like Individuals

A study on a number of traits in rhesus macaques revealed the dynamics of coalition formation in these despotic groups (Higham et al., 2010). These data suggested in total that coalitions are members of like individuals who join forces in order to better contest with highly ranked individuals. Some of these characteristics include rank, social affiliations, group residency length, and biometric measures like body size, canine length. Interestingly enough, this paper uses different descriptions for its behaviors, defining all-up coalitions as revolutionary and all-down as conservative. In doing so, these subtle distinctions imply that these behaviors' potential effects are integral to our understanding of them as well as our definitions of them.

It was noted that the coalitions of this free-ranging group were all-up, revolutionary, and (in many cases) rank-changing. These events often ousted dominant members from the group, precipitating increases in rank for lower-ranking males. However, it is important to note that the group members who form these

coalitions tend to be mid-ranking members, whereas low-ranking members do so less frequently. While this may likely be related to the costs of these behaviors, given that these low-ranking members would have lower competitive ability and less of a chance for success, one should consider whether these individuals have less to benefit from such a position or if factors unrelated to competitive ability may increase social benefits.

In other words, mid-ranking members may be more well-acquainted with group members, so their increases in rank may be more welcome, whereas increases in rank on the part of low-ranking males may have fewer social ties and means for increasing their own rank during a period of hierarchical instability. After all, it was also noted that coalitions are more likely to form between friends and acquaintances than would occur simply due to chance. As this has been demonstrated, these low-ranking males would have few mid-ranking affiliates with which they could bolster their competitive ability. This is exacerbated by the finding that many of these low-ranking males were immigrants who had few ties to the group and were, therefore, less likely candidates regardless of any physical abilities.

It is important to note the ecological anomaly presented by macaques living in Cayo Santiago. Unlike their endemic South Asian range, the environment provided by this Caribbean island presents abundant resources that would usually limit group size in rhesus macaques in their natural environment. As a result, mating pressures are reduced, as larger group size inhibits alpha males' ability to hoard access to females. There are simply too many females to do so for. As a result, many of these males do not disperse to other groups living on the island, as these resources are

relatively stable and are more certain than trying to assimilate into a new group after puberty. A new dynamic exists in this group that normally would not be present: aggression between natal and non-natal males. As noted before, rank coalition members were often similar with regards to their group residency length. Due to this despotism that favors natal males, the authors predicted that the many mid-ranking coalitions that targeted high-ranking males would tend to consist of older, stronger coalition members targeting younger, weaker dominants whose rank is solely based on their natal status. This can be seen in some of the biometric data recorded, as the canine teeth of these individuals were longer than those who were not commonly found in coalitions.

Physiological Consequences of Aggression and Coalition Formation

As in the previously mentioned cases, the neuroendocrine impacts of these behaviors and their effects on anxiety and emotional states provide evidence for an endogenous mechanism by which social behaviors may be regulated. One study found endocrine correlates with aggression in Japanese macaques, specifically looking at female-directed aggression by males (Barrett et al., 2002). While high-ranking males and low-ranking males did not show significant differences in aggression, high-ranking males had much higher levels of cortisol. This contradicts the common suggestion that subordination is stressful in primate societies, as these high-ranking males showed more stress. In questioning what may cause this difference in cortisol production, the authors hypothesized that mating-related stress may be involved, as individuals in this study showed that mounting was more frequent in individuals with high cortisol levels. Another study in rhesus macaques

also found that the significant difference in glucocorticoid concentrations seen between low and high rank was only found during periods of mating instability (Higham et al., 2013). No endocrine difference was found outside of the mating season. It appears that a stressed response may be a cost necessary to reap the reproductive benefits of being a highly-ranked male. Also, it may be that these endocrine changes associated with mating seasonality enforce the coalitionary behaviors seen here, providing an endogenous stressor that would facilitate heightened aggression in order to have access to females and hinder others' access. However, this may result in occasional aggression towards females.

Grooming and Coalitionary Behavior: Social History as a Predictor

A study by Schino (2007) attempted to address the relationship between aggression and grooming in Japanese macaque females. It was noted that low-ranking females in these groups were the most common groomers, often grooming the high-ranking females of the group. It was also observed that these females often groomed the group's more aggressive females, suggesting that grooming is a method by which aggression towards low-ranking members can be reduced, a method for appeasement. However, it was noted that low-ranking females did not tend to groom those who behaved most aggressively towards them. This may suggest that individuals groom those who will give support to them through coalition formation, in order to defend themselves from aggressive, high-ranking females who they tend to avoid and choose not to groom.

A following study found data that supported typical conclusions that both grooming and agonistic support (coalition formation) are often reciprocated by the

other members of these dyads. It was also noted that individuals that groomed another most were more likely to receive social support from them and that individuals who sometimes formed coalitions with another group member were more likely to groom them. This suggests that grooming is not only a mechanism for social cohesion and relationship formation resulting in valuable affiliations. It also can serve as a method of social payment and gratitude after such an event occurs.

Oddly enough, this was also one of the few studies on coalition formation and aggression seen between female macaques. It was found that these females demonstrate long-term ability and tendency to reciprocate these prosocial behaviors with further prosociality. The authors note that this long-term ability to return favors and maintain social bonds based on the value of received requires two cognitive abilities. First, individuals must remember who has behaved prosocially towards them. Second, individuals must be able to compare the behavioral services they have received from other group members in order to determine who is more valuable and base their behavior off of these estimates.

The authors suggest that emotions associated with these partnerships may influence their behavior, further perpetuating pre-existing relationships with grooming and agonistic support. This goes against the notion that primate behavior is primarily a product of immediate behavioral responses, such that coalitions would be formed more often between individuals who make better coalition partners rather than individuals with whom one has had an extensive social history. However, it appears that both of these factors are at play. While those who are more affiliated are more likely to form a coalition, it is also the case that better coalitions are more likely to

succeed. Given these two pressures, it seems likely that coalitions are formed between affiliates who solicit aid from their most competitively able and available acquaintances.

I wonder whether the frequency and duration grooming, given its potential payment function, would differ depending on the rank of these common coalition members. It seems possible that the extent of grooming may be related to this difference, such that low-ranking members have to engage in more prosocial behaviors in order to have access to a social service as costly as coalition formation. Another question stemming from this is whether any factors regarding the success of aid solicitation can be discovered. Why are certain subordinate members more able to receive aid from higher-ranking, stronger group members? Also, given that this study involved the behavior of females who almost always stay in the natal group, how fluid are these relationships throughout life? It seems possible that coalition formation in females can be dependent on factors relating to their own kinship as well as the kinship of others, i.e. helping their own offspring as well as the offspring of their non-kin affiliates.

This question brings me to the concept of intervention. While some behaviors that elicit the involvement of a third party result in further aggression against a target, there are many instances where a third individual is able to stop aggression with their presence without any immediate bias towards any of the individuals. It is important to compare coalition formation and intervention, because the differences in effect indicate the many social pressures that influence behavior in macaque species. Coalition formation indicates environmental pressures that favor either the exclusion

of new individuals (conservative, social maintenance) or the ousting of despotic leaders (revolutionary, social reformation). While these behaviors do result at the expense of the target, the coalition members (if successful) share mutual benefit from this interaction, both receiving a greater share of the group's resources than they would have before. In intervention, rather, there is no need for removing resources from another, indicating a more stable social ecology based on resource availability, promoting social cohesion without aggressiveness and the possibility of altruistic interference against any existing aggression.

Intervention

The behaviors seen after conflicts demonstrate that the presence and participation of third parties is highly conducive to reduced aggression and reconciliation. One such study in stump-tailed macaques (Call, 2002) noted affiliative behaviors that occur after a conflict and addressed a few trends in whom these behaviors targeted and/or involved. Sometimes these individuals engaged in the conflict dyad with allogrooming; other times a sexual bout ensued. In analyses that separated sexual and non-sexual behaviors, it was noted that third parties did not tend to bias their prosocial behaviors towards their own kin who have been aggressed upon. Third parties were more likely to groom the aggressive opponents of their kin, when their kin were the primary victims of aggression in the conflicted dyad. In this way, relatives are engaged in the reconciliation of those with whom they share genetic information. This, to me, suggests that social ties, though established by

social histories between individuals, have transitive properties and can be shared amongst kin networks.

Also, with regards to sociosexual behaviors, third parties most often directed their intervention behavior towards unrelated individuals, regardless of any relationship of kinship. This supports suggestions that individual macaques are able to recognize and discriminate the kinship status of individuals, such that those who are related are not as viable partners for sociosexual activity. Also, given sociosexual activity's function in reducing the likelihood of aggression after conflicts, it may not be necessary to perform these behaviors with one's own kin, as there is not as much of a likelihood that aggression will continue. Also, this suggests that third-party individuals may have an understanding that they may be victims of aggression after such a conflict. It may be interesting to see whether individuals tend to behave aggressively towards a group of related recipients.

Behaviors directed towards the victim of such conflicts tended to be sexual in nature, as they received less grooming from all parties involved, but were most often engaged in sexual reconciliation, though less likely with related partners. It was also noted that, though they often engaged in these behaviors with their own opponents as a form of reconciliation, they were less likely to interact with third-party kin of their own opponents. By separating their analyses based on behavior, the authors were able to note how the roles of victim and aggressor are important in regulating behaviors, especially with regards to third parties.

All of these above described behaviors indicate how third parties are important in the period after a conflict. Their presence may reduce tension, as they

groom aggressive individuals and decrease likelihood that further antagonism will ensue. On the other side of the coin, the individuals involved in the dyad may respond to such an intervention of a third party opportunistically, engaging with the third party member in ways that best allow for reconciliation between the two parties. This also introduces the idea that these interventions are merely redirections. By providing group members with a social reward like grooming or socio sexual behavior, these third party individuals inadvertently dissuade others from continuing their aggression. Regardless, this behavior is seen often enough that the role of these third party members must be addressed, as their behaviors, often based on kinship and social history, provide a cooperative, sometimes-altruistic mechanism for aggression reduction.

Kintervention

In a series of experiments on Japanese macaques (Chapais, 2001), a few relationships were found in how maternal kinship lineage affects the behaviors seen in intervention. In these experiments, juvenile macaques were placed in conflicts with dominant individuals. Related females could either intervene or disregard this interaction. Contrary to what could be assumed based on genetic relatedness, mothers and siblings were not the most common interveners, as age also appeared to be a contributing factor. Great-grandmothers had the highest rates of intervention for both one-year old and two-year old juveniles. The researchers suggest that this may be due to a minimized effect of collateral relatedness on the behavior of individuals, such that direct kinship (without siblinghood) breeds familiarity. In this way, juveniles would be more familiar to their great-grandmothers than their equally-related but

less-responsive aunts. However, I suggest that nepotism is the primary factor here. Great-grandmothers are not more familiar with these juveniles; they simply have fewer costs associated with intervention. As they are well-respected females with comprehensive social ties, they have a greater likelihood of inducing a rank reversal than a less esteemed aunt. It would be critical to replicate this study in a less nepotistic system, as these behaviors may differ such that kinship is more of a contributing factor than its interaction with age and dominance.

However, there are instances that demonstrate the effects of kinship are very convoluted. As noted, the differences seen in aunt and great-grandmother intervention rates demonstrate the extent to which external factors mediate these behaviors. The trend seen in the previous study is not about relatedness, it is about rank and age and the benefits one has from having much older kin who can provide protection. Another such problem that is difficult to determine is how familiarity can differ amongst kin. Do direct lineages spend more time together than those that are removed by siblinghood? One way to address purely genetic contributions to social behavior is to test the effects of paternal kinship.

One study tested the effects of paternal kinship on intervention rates in adult female rhesus macaques (Widdig et al., 2006). The researchers noted that these females directed supportive interventions that involved maternal half-sisters significantly more than those with paternal half-sisters or unrelated individuals. In fact, support levels for paternally related females were significantly lower than those for unrelated individuals. Also, females were less likely to antagonistically target higher-ranking, maternally related females but not at low costs (when the target was

of lower rank). This suggests an interaction between kinship and rank, such that related dominants are more effectively dominant over the behavior of kin than non-kin. However, total antagonistic targeting analyses showed that maternally related kin accounted for the vast majority of antagonistic interactions. Also, though no relationship was seen for support, females avoided targeting paternally related kin in both low-cost and high-cost interactions.

Given that maternal half-sisters are more closely affiliated, it seems fitting that this would preclude less outwardly antagonistic interactions and more supportive interventions between these individuals. Given their spatial proximity, these individuals are more likely to target one another, as there are more opportunities to do so. Also, the kin targets of these interactions were often older females, who are lower in rank and less able to remain dominant in such interactions. Because of this age difference, it seems likely that kin support is primarily a function of living in a similar developmental environment with the same or closely related mothers. In this way, kin who are genetically related but different in age are less likely to act upon their relatedness and increase their inclusive fitness through such support. It is also possible that these females, being older, are less valuable to the group because they are less likely to have offspring. In this way, agonistic support by kin may further be biased towards related females who are more likely to reproduce. While kinship breeds spatial proximity, it leads to aggression as females primary kin-based affiliations are with those of similar, more-valuable age classes.

This calls the nature of intervention-based altruism into question. As these females solely directed their behaviors to other individuals, it appears that selfish

motives may be at play. These more closely related females have more extensive histories of grooming and other affiliations. As a result, they are more likely to engage in alloparenting in a nepotistic network where kinship is highly important for the success of infants. If these behaviors are so selfish, where is there room for altruism in this behavior? For that, it is important to look towards the behaviors seen directed towards paternal kin. First, it is important to note that paternally-related females spend more time with one another than unrelated individuals. However, they do not appear to show support to one another in agonistic interventions. The researchers suggest that this may be because paternal kin are less likely to be similar with regards to rank and their intervention-related abilities.

I further suggest that learning and development are at play. Females of maternal kinship and similar age are more likely to have formed affiliation in their early years and have shared close proximity due to the presence and guidance of their mothers. Such support may have been demonstrated by their own mothers in early life; these females, when young, may have learned to support their maternal siblings, particularly when they were younger, as seen here. It is also important to distinguish the antagonisms seen here. While antagonisms were generally demonstrated towards maternal kin, it may be that these more affiliated individuals perceive these bouts as less threatening. In other words, antagonism towards non-kin may be more a method for protection whereas aggressive play directed towards kin may be a redirection of the situation using their play as a distracter.

Given that all of these modes of intervention with kin involved stop an aggressive action involving kin, they may increase the social stability of their most

highly related networks in a cooperative manner. In order to show this, it would be best to note affiliative behaviors between members of these triads and note whether differences can be seen after such interactions. If these individuals show more affiliation after such interventions, this behavior's role in facilitating longitudinal cooperation may be demonstrated. Such facilitation would be primarily based on cost of such cooperation, based on the rank, kinship, and additional competitive constraints on cooperation of all involved parties. Cooperation may be tied to self-interest; however, the costs cooperation may incur suggest that there are instances in which cooperation is done to benefit the interest of a valuable partner.

Sex and Intervention

One study on the rhesus macaques of Cayo Santiago hypothesized that interventions involving male and female members may be related to rank and the reproductive fitness of males (Kulik et al., 2012). First, it was noted that the most commonly intervening, supportive males were the highest-ranking males of the group, who, by nature of their rank, are more likely to have access to females. These males were more likely to support those whom they had more social ties with. These males also more often supported females and targeted males who had targeted females. While it has been generally demonstrated that females are the primary coalition-formers in highly nepotistic species, it was noted that these high-ranking males did so at rates similar to those for the group's female cohort.

However, despite these otherwise compelling data, no correlation was demonstrated with fitness. There was no correlation between female support and siring success. The researchers noted that, perhaps, these behaviors do not result in

mating success because of the low-to-moderate mating skew seen in this species, such that dominance is not critical to the fitness of males. Also, if it were the case that intervention on the part of males was associated with reproductive success, males would be more responsive and intervene more often when fertile, swelling females were being targeted. However, this model does not account for whether these males were more likely to exhibit mating with females involved in these interactions. Given the frequent sexual behaviors, conception is less of a relevant indicator for success, especially given the lack of paternal input by males. Furthermore, supportive males who do sire these females' offspring do not exhibit any more parental behavior to their offspring than those who did not intervene both before and during the mating season.

However, this causes me to ask the question of why males would prefer to behave towards females. This suggests that these matrilineal groups result in male hierarchies that are highly dictated by female behavior. Instead of supporting females for sexual and reproductive reasons, males may be doing this for social reasons. As females constitute a large proportion of the group's membership, it is wise for these males to behave prosocially towards them, as these relationships open doors for further valuable relationship formation that allows for increases in dominance rank. Though the tendency may be to assume that male-female behaviors are dictated by reproductive needs, it may simply be that having relationships with females is key to building trust from a group of individuals who have the power to regulate the rank of males. The evidence that males more often support females during mating seasons may further perpetuate this notion. However, it may be the case that this bias in

seasonality is indicative of males' increased rank instability during a period of time where mating does occur. While their behaviors may not result in greater success, it may be doing so is more conducive to (group) success than not supporting females during antagonistic interactions.

Also, it is important to note the plasticity of this system. The group observed in these interactions changed dramatically in the twelve years following this study, eventually comprising of the disproportionate number of related males mentioned earlier in this chapter. While the triadic interactions noted in this study on male-female interactions were primarily all-down interactions involving a high-ranking male supporting an (oftentimes) receptive female, the coalition behaviors seen twelve years later included a large number of all-up coalitions on the part of mid-to-low ranking males. This suggests that there was a change in the dynamics involving rank and mate availability.

Intervention: Peace or Aggression?

I mentioned Petit and Thierry's paper on Tonkean macaques in the previous chapter (Petit and Thierry, 1994). This study demonstrates how intervention is critical for the preservation of social relationships after the occurrence of conflict. This study separated peaceful and aggressive interventions. Peaceful interventions typically included play-like behaviors: lipsmacking, clasping, mounting, grooming, etc. Aggressive interactions involved physical harm, including bites and other blows. While it may be generally stated that these behaviors were biased towards the dominant individual in both cases, some differences prevail between these behaviors. First, peaceful interactions predominate the intervention landscape, indicating that

preservation of relationships between the members of the triad is more desirable than a more biased, harm-incurring alternative. It is because of this cost to social behavior that kinship is more heavily tied to aggressive interventions. The likelihood of aggressive intervention was higher when kin were being aggressed upon and targeted. Furthermore, a study in rhesus macaque groups found that separate groups showed different tendencies with regards to intervention styles and that these styles were related to levels of severe aggression (Beisner et al., 2013). Groups whose interventions were peaceful, impartial, and halted aggression towards subordinates showed lower rates of severe aggression than those that did not.

However, seeing as how the peaceful behaviors mentioned here were quite capable of halting aggression, doing so twice as often as aggressive interventions, this raises the question of why individuals would risk severing a social relationship in order to help their own kin or non-kin affiliate. While this may suggest that individuals perceive a greater risk when their own kin are being threatened, but it may also suggest that enemies who tend to attack one's kin are less valuable individuals to have in one's own social proximity. While many studies acknowledge the intergroup and intragroup competitive forces that govern behavior, the recognition of smaller groups within social organization has been less frequently addressed. By self-sequestering into groups of like individuals with valuable social histories, altruism results. Like in the case of humans, it seems like only so many valuable relationships may be possible such that sub-groupings are necessary.

While it may be an anthropomorphic suggestion, this may also be at play in macaques. While investing in the livelihoods of all other group members

indiscriminately may suggest completely egalitarian societal functioning, this is not quite as possible, as a series of small reciprocated acts results in less stability for one's benefits than larger investments in a genetically similar cohort of valuable relationships. Though aggressive interventions like those seen in the Tonkean macaque system may result in further aggression, these actions are not socially dangerous. Either the aggressed individual is unaffiliated or has desirable resources. For social maintenance-based societies, this may result in the aggression to those with whom individuals are unfamiliar; for social reformation societies, this may result in aggression towards those who are familiar, but whose resources are desirable. Furthermore, though interventions often are directed by third-party members towards grooming affiliates, it has also been shown that individuals will often intervene on behalf of individuals with whom they have histories of aggression (Silk, 1994). This further questions the fluidity of aggression; it contextually may be considered play or dangerous. In this way, descriptions of aggression and play may only vary based upon the response of the targeted individual, further questioning the intention of (pro)social interactions. Regardless, the plurality of peaceful interventions and interactions suggest that inclusiveness and cohesion are desirable and increase the fitness for individuals and groups, so long as resources are ample and (semi-)equally available.

Resolution and Reconciliation

While many aggressive conflicts incite the intervention of a third party, some antagonism results in reconciliatory behaviors between the members of the conflict. They may begin to groom one another after such aggressive interactions. One study

on these behaviors sought to determine the effects of three relationship descriptors on these behaviors: value (fitness benefits of the relationship), security (the regularity with which prosociality occurs), and compatibility (chance that the individuals will compete for the same resources) (Majolo et al., 2009). Ultimately it was determined that these three factors were related to the behaviors seen in reconciliation. First, reconciliation was more likely when the individuals involved in the conflict often groomed one another historically. Conversely, when reconciliation does not occur, it has been shown that former grooming relationships were hampered, such that grooming rates between post-conflict partners were lower than they were previously.

In addition to grooming, two other factors were incorporated into a model for predicting the likelihood of reconciliation. These factors included frequencies of aggression and tolerated co-feeding. In the case of aggression frequency, it was found that increased frequencies of aggression were associated with positive conciliatory tendencies. This continues the notion mentioned previously in this chapter that affiliates often behave aggressively towards one another. This incited the authors to compare the aggression intensity (mild to severe) exhibited between affiliate and non-affiliate dyads; however, no relationship with intensity was found. By nature of their proximity, affiliates are more likely to behave aggressively towards one another. Their proximity also fosters friendliness and an increased likelihood of reconciliation when aggressions do occur. This calls into question why such aggression would occur in the first place if these relationships are highly valued and aggression would require additional reconciliation costs in order to preserve such a relationship. It could be found that certain pressures result in these behaviors for some immediate benefits

(food or mate access), while the reconciliation period allows for the preservation of a relationship.

There are also effects that do not relate to the individuals at hand. When conflicts are over more highly valued, less shareable resources (food or mating partners), it is less likely that conflict partners will reconcile. However, this calls into question whether reconciliation must be immediate in order to be considered reconciliation. While, as noted before, affiliative interactions between friends may reduce in frequency after bouts that were not reconciled, it could be noted that reconciliation may be delayed in these cases. Time is an important resource to acknowledge. Given the long time investment devoted to social cohesion in all groups of macaques, social maintenance can wait. Food and mates are less stable resources than any valued relationship. Therefore, stopping to reconcile with even close kin would reduce the likelihood of receiving a valued resource. All in all, this study notes many of the factors influencing reconciliation and how behavior is a product of trade-offs between immediate resource needs that foster aggression and longitudinal social needs that foster friendliness and reconciliation.

It is important to note also how context can affect trends regarding reconciliation. A study in long-tailed macaques (de la O et al., 2013) found that reconciliation rates in this captive group of macaques were much lower than observations have noted in the wild. The levels of reconciliation were more similar to those seen in despotic species. It appears that the resources presented in a captive environment are more conducive to pressures that would lessen the likelihood for reconciliation. Regardless, reconciliation was still a common response to post-conflict

stress, suggesting that relationships are no less valuable. Environmental pressures influence whether immediate resource availability or longitudinal social gains are perceived as having greater benefits relative to cost.

Post-Conflict Distance and Reconciliation

One study examined the nature of post-conflict distance (Call, 1999). Based on research in both stumptail and rhesus macaques, it was found that post-conflict (PC) individuals were more likely to be in closer proximity than matched control (MC) individuals. In addition, this study noted that individuals for whom the difference in distance between post-conflict and matched control observations was larger were more likely to reconcile. When PC and MC distances were more similar, there was a reduced likelihood of reconciliation in both species.

This seems very logical, as proximity would allow for interactions like grooming to follow a bout of aggression. However, there was not a clear relationship solely with distance, as it is important to note that PC distance did not correlate with the likelihood of reconciliation. Only the difference between PC and MC distance was associated with an increase in the likelihood of reconciliation. The researchers also noted that there were differences between the species, as there was an increased likelihood of reconciliation for stumptail pairs than for rhesus pairs at any inter-opponent distance. The researchers here suggest that these result from differences between these species with regards to behavior. While rhesus macaques often chased one another for extended periods as part of their conflicts, chasing was less common in stumptails, who often slapped one another in close proximity. Also, stumptails exhibit unique affiliative behaviors after conflict like bottom-grabbing. The

researchers suggest that there are species differences in conciliatory intent that influence their proximity and the likelihood that reconciliation will occur. The researchers suggest that this is not due to group composition and likelihood of kinship, as these statistical correlations demonstrated species differences even when only non-kin pairings were used in analysis.

I suggest that these differences based on non-kin pairings do reflect the social organization of the groups (though not its membership). The proximity seen in the females of stumptail macaques suggest that these females more commonly have valuable relationships with one another and that the differences seen here are indicative of whether cohesive forces in female social organization differ across these species. In order to best determine the roles of species and socioecological environment would be to compare the extent of reconciliation differences in kin and non-kin dyads across these species. It would likely be found that the difference between kin and non-kin reconciliation rates in rhesus macaques would be greater than that in stumptails. It may also be found that a larger difference in reconciliation rate between non-kin would be found between the species than between kin. Rhesus macaque social organization may reflect higher value of affiliations based on kinship as opposed to comparatively less secure non-kin relations.

Kinship and Reconciliation

A paper on the effects on kinship in species confirmed those hypotheses (Aureli et al., 1997). In long-tailed and rhesus macaques (despotic style), it was found that kinship was a greater indicator of the likelihood of reconciliation than was the case for Barbary macaques (tolerant style). Though, in general, Barbary macaques

reconciled with their opponents more than the other two species, the differences seen between non-kin and kin reconciliation rates were less pronounced in this species. However, these differences were not associated with the number of kin in these groups, suggesting control by other ecological variables. Again, these researchers note that these differences are likely not due to contributing factors of the environment, representing differences in the repertoire of behaviors seen in these species. In doing so, they discount the possibility that mate availability has an effect on the behaviors seen in this system and assume direct roles of kinship without differentiating non-affiliates and affiliates in their study. Their mate availability assessment suggested that it was not a contributing factor but did not account for whether high-ranking males had more control over mating resources, assuming sex ratio as an accurate metric of mate availability for all group members included in the study.

However, a number of macaque studies note that juvenile reconciliatory behavior shows no consistent kinship effects (Cords and Aureli, 1993). This suggests that behavior based on kinship is a learned, developed phenomenon that is not as present in species like Barbary macaques. Barbary macaque mothers are likely to affiliate with non-kin group members as well as kin. Therefore, juveniles learning from their mothers are less likely to discriminate their behaviors based on kinship.

Stress and Emotion as Mediators of Reconciliation

A study in long-tailed and Barbary macaques found that individuals often showed self-scratching behavior after conflicts, doing so to a greater extent after conflicts with close affiliates (Aureli et al., 1997). The authors hypothesized that this

stress-inducing uncertainty in post-conflict relationships would result in a conciliatory tendency.

In her dissertation on post-conflict reconciliation, D.A. Smucny (2000) addresses the endogenous, physiological effects of reconciliation in rhesus macaques. These include heart rate changes and chemical changes associated with emotional response. For heart rate, it was determined that post-conflict reconciliation increased the rate at which individuals involved returned to pre-conflict heart rates. A similar effect was found across all forms of post-conflict affiliation, regardless of whether or not these prosocial actions occur between the aggressor and victim. All in all this suggests that the body's response to such aggressive acts is unfavorable and that social interaction after aggression helps return individuals to stability. In this way, individuals favor sociality when relationships are stressed.

However, the roles of third party and conflicted party reconciliation differ not only in their social effects but their physiological consequences. When low- and high-intensity conflicts were separated, it was shown that reconciliation resulted in a higher heart rate reduction rate than third party affiliation for high-intensity conflicts. However, though these greater reductions may occur, when post-conflict macaques have the ability to affiliate with a third-party individual, they may take this over attempting to reconcile with their opponent who may still aggress upon them. For low-intensity conflicts, it was found that the effects of reconciliation and affiliation on individuals were somewhat delayed. Smucny hypothesizes that this may result from the finding that low-intensity conflicts can escalate, such that there is more stress and risk associated with affiliating after a low-intensity conflict. Another thing

to note is that these low-intensity reconciliations were more successful in returning individuals to their pre-conflict heart rates.

Smucny goes on to say how emotional responses should be used in the future as an indicator of relationship quality, as high-quality relationships will result in greater stress reductions for the individual at hand than those of lower quality. It may be of interest to note how these differ based on the rank and genetic relatedness of those involved. In order to best understand the relationships involved, a wealth of data need to be considered in order to fully understand what makes relationships valuable such that affiliation with an opponent is more quickly stress reducing than affiliation with another person. This phenomenon is all too common in humans. One may find solace in talking to others about their interpersonal qualms, doing so rather well when these problems are relatively small. However, when relationships are severely strained, the most surefire way to reduce this stress is to resolve these difficulties with the individual involved. Non-human primates appear to be weighing the costs and benefits of post-conflict choices and behaviors in a manner similar to humans.

Conclusion

The nature of coalition formation as it relates to the forces involved in altruism is quite nuanced. As demonstrated by this chapter, coalitions may negatively affect targets, but there are opportunities for the biological definition of altruism to occur. Individuals may offer their competitive ability in order to benefit others at some cost to them with no known benefits. However, these seemingly unknown benefits for those who enter coalitions suggest that the nature of social organization

allows for such actions, as less dominant individuals can survive an oftentimes aggressive social landscape with the help of their affiliates and dominant individuals can keep their dominance by maintaining relationships with subordinates. Macaque social organization is regulated both top-down and bottom-up.

The three different scenarios reflect the varying nature of interest that reflects aggressive behaviors: those in which one individual or group is successful and the other fails, those that are interrupted by an aggressive third party member, those that are interrupted and become peaceful due to the intervention of a third party, and those that become peaceful without the aid of a third individual. Peace-promoting behaviors are ecologically mediated, as conditions must favor social cohesion over relatively small, immediate fitness benefits in order for them to happen. It is the occasional need of some individuals, however, to use the power of additive competitive ability in order to change the rank of dominant individuals and redistribute resources through reformation of social organization. These criteria preclude such behaviors that would lead to social reformation. It is important to note, though, that these behaviors are relatively infrequent, even in “despotic” species. Social upheaval is not frequent, as individuals do so only when conditions would favor such a change: when despotic leaders have a particularly harsh hold over resources and mid-ranking subordinates have strong affiliations that would favor coalition formation. It also does not last long, as these periods of instability soon reach equilibrium, as new rank relations begin to settle and become stereotyped.

However, if social cohesion is so desirable for most of these groups, why does aggression occur at any level? It appears that such aggressive actions are sought in

order to preserve more valuable forms of cohesion to the individual, relationships with affiliates and kin. The valuable relationship hypothesis holds especially true here. In a group with especially dominant individuals, subordinates must rely on their affiliations in order to best acquire resources and survive. While it has been hypothesized that organized aggression through coalition formation may influence broad rank changes, a study in bonnet macaques demonstrated that rank changes (though small) were not associated with the frequently formed coalitions in the study group (Silk, 1993). This does, however, come at the cost of severing potential relationships with targets. That is why reconciliation is a powerful behavior that helps lessen the costs of helping one's allies.

It seems that aggression is allowable due to the very nature of groups, as these individuals may aggress upon one another given adequate means for conflict reduction. Intervention is one such powerful mechanism. It has been shown that such group policing by intervening members is a powerful force for influencing and stabilizing social niches (Flack et al., 2006). When rhesus monkey group policing was reduced, social cohesion lessened severely and the affiliative networks within groups were greatly reduced in size. Subgroups became more clumped and less inclusive. Also, as the removal of these behaviors caused large behavioral consequences, the plasticity of dominance style is again demonstrated.

There may also be elements of irrationality reflected in these behaviors as well. After all, certain groups have demonstrated a tendency to attack one's own kin. This is not adaptive, as these behaviors can only harm those close to them. Is a basal level of aggression indicative of a healthy macaque or macaque group? Given that the

behaviors seen in play are often construed as aggressive, as in the case of the railroad tracks monkey of Kanpur, how can human observers best discriminate the intent of potentially harming behaviors? Does aggression towards kin have unique characteristics that would not be seen otherwise, or are kin just more willing to accept more aggression?

This questions the validity of perceiving aggression wherever such behaviors exist, as it is hard to discern intentionality on the part of the aggressor. In considering human behavior, I can recall that most of the human fights (physical and verbal) I have seen have been between (oftentimes close) friends and family. The mere exposure between individuals presents a statistical likelihood that aggression will occur at some point. However, reconciliation and intervention are mechanisms by which damage can be controlled. I have seen parents break up fights and seen combatants eventually shake hands upon reaching a consensus. Maybe this is not too far from the case of macaques. Aggression is an inherent response to stressor, an impulse to protect oneself that often comes at a cost. The potential for peacemaking in all primates suggests that primate social organization is unique in that such a level of reliance on other group members is not only desirable but necessary. A need for social cohesion is manifest through these behaviors. Seemingly antagonistic behaviors are not the opposite of prosocial behaviors, they are socio-ecological reactions to more severe resource pressures that come at social costs that require reconciliation or create a fortunate, desirable period of instability.

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Conclusion

Primate Behavior and the Origins of Altruism and Cooperation

All of these previous examples present a case for altruism and cooperation as being profoundly developed in primates. Altruism and cooperation are highly nuanced, as the costs of benefitting one's allies often leads to reciprocated benefit for the altruist, through reciprocation or kinship-related gains. Primates also are capable of dismantling certain social relationships through aggression. However, cooperative aggression often results in the preservation of individual's relationships with valued group members. Given that these complex behaviors are present in our evolutionary relatives, comparisons to human behavior are common and often insightful and raise important questions about the origins of these behaviors and how these reflect the environments and actors of both the distant past and the ongoing present.

By nature of social living, such behaviors are seemingly necessary. The origins of cooperation require a highly developed social system, with social memory and methods of communication. In the evolution of groups that have complex social niches, different roles must be established and preserved in order for groups to survive and respond to a changing environment (MacKinnon and Fuentes, 2011). Thus, behaviors that allow for social maintenance (grooming and co-feeding/foraging) are pervasive. In addition, given pressures from potential predators, group living has further importance, as behaviors that would prevent harm to group members become desirable and potentially adaptive. As a result of this social complexity, relationships became critical to survival. Variation amongst groups with regard to their composition, relationships, and resources determines the behaviors that

are most valuable to the survival of group members, as well as that of the group. Also, by bonding with group members, social niches can be reformed, as each new relationship changes the social landscape of a group. Social behavior can become more plastic as a response to this complexity.

As a result, some behaviors and abilities are vital to the survival of these groups. Individuals must be able to recognize the many faces within their group's membership and must remember the histories they have with group members in order to determine whether cooperation with these individuals is desirable (Moreira et al., 2013). It has been hypothesized that, as groups become larger, there is a greater pressure to remember these individuals in order to best coordinate one's social behaviors. In addition to the ability to remember social histories and act upon them, some communication abilities manifest in order to best transmit valuable information to one's social affiliates or simply to strengthen social bonds (Gaspar et al., 2011). Methods of communication such as facial expression inform others about one's emotional state or social intentions. As a result, routes to strengthening social bonds become more robust, thus precipitating a further increased likelihood of altruistic and cooperative behaviors.

Macaques are an ideal group to look at when exploring the dynamics of the origin, evolution, and plasticity of these behaviors because of their diversity. They demonstrate cultural differences, as certain groups display novel behaviors that others do not and show different behavioral trends dependent on who in the group is considered valuable. They are ideal candidates for demonstrating how different group dominance styles (despotic and egalitarian, social reformation and social

maintenance, etc.) are a product of how constrained resources are divided based on a group of certain size and membership (Flack and de Waal, 2010). As a result, different distributions of power arise in different groups within and across macaque species. As mentioned before, these reflect the dynamics of early human societies, as hunter-gatherer societies exhibit behaviors much more like agricultural societies (Ciani et al., 2012). In this context, it is more easily demonstrated how altruistic and cooperative behaviors are plastic across all primate species. They are products of social systems that are constantly reacting to changes in the composition and needs of groups.

Given different resource needs, sex ratios, and age distributions, behavioral costs and benefits are constantly in flux, and these inputs affect the dominance structure observed within and across groups (Broom et al., 2009). As a result, it may be wise to consider altruism in relative terms. What is altruistic to a rhesus macaque may be different than what is altruistic for a Tonkean macaque. The former may value the aid of an agonistic intervention from a strong, high-ranking kin member, while the latter would be more likely to demonstrate a peaceful intervention in order to preserve a greater number of relationships. Because of their different socio-ecological contexts, neither can be considered more altruistic than the other, regardless of what mathematical models of costs and benefits may suggest. Altruism could therefore be a common trait amongst all primates descending from a common ancestor. The repertoire of macaque behaviors depends more upon social contexts than the genetic evolution of different social and cognitive abilities.

Altruism, Cooperation, and Human Behavior

While non-human primates show profound memory capabilities that allow them to retain social memory and information and to act accordingly upon it, human behavior embodies this notion to its extreme. Information is passed so easily in modern human societies, as social media allows individuals to know so many previously unavailable details of their acquaintances' and friends' lives. It has never been so easy to judge other individuals and to decide our friendships based on our judgments. While this may make for a seemingly hostile social realm in which every choice is held under scrutiny by one's peers, such exchange of information is highly desirable and may allow for friendships that would otherwise have been unlikely or impossible. Social solidarity and kindness can be as easy as clicking a "like" button. Regardless of how silly these pointless actions may seem, they affect recipients and the way in which they interact with the world. Through such interconnectivity and a rising standard of living for some populations, affiliations are less costly than they have previously been.

Stefan Klein described this in *Survival of the Nicest* (2014), stating, "the more people around the world know about and depend on one another, the higher the benefits and the lower the risks of selflessness." This is not to say that larger affiliation networks would render rhesus macaque populations less despotic; it merely demonstrates how a population's behavior can change when social risk and competition are reduced by the safety that social knowledge and awareness provide.

Similar concepts to those previously described are quite entangled in human social behavior (tendencies toward helping kin, reciprocity, formation and maintenance of valuable relationships, etc.). It is important to address both elements

of altruism that are unique to humans and to recognize how research in human behavior can provide insight into the nature of when and between whom altruism and cooperation occur.

Humans tend to behave differently towards altruists than towards those who do not behave altruistically. One experiment in humans found that those who behaved altruistically were more often trusted than those who did not (Barclay, 2004), reminiscent of how macaques who did not vocalize upon discovering food were met with aggression (Hauser, 1992). Cooperation precludes a good reputation, allowing these individuals to reap the benefits of group living and sociality. This is true for humans and macaques alike. While both macaques and humans base their behavior towards individuals based on both the size of the gifts they receive and on their social histories, it is important to note that humans can better understand others' reputations than macaques and have opinions of (and prejudices against) other individuals that extend well beyond their social utility and history.

While it is beneficial to be altruistic, it is also beneficial to be friends with altruists. One study on altruism in humans asked college-aged students to rank 100 individuals they know with regards to how close they are to these listed people (Yi et al., 2010). The computer program then asked the subjects to choose to either give one of their ranked friends \$100 or receive some money themselves. As would be expected, these individuals were more likely to give this money reward to their friend when the computer randomly chose someone who was ranked quite highly than if the computer chose a low-ranked individual. This furthers the extensions of the valuable relationship hypothesis, demonstrating how individuals are more likely to behave

altruistically towards those whom they value and with whom they likely have histories of altruism and cooperation .

This study mentions a factor that is not easily tested in macaques: time. In certain trials, individuals were told that these rewards would not be given immediately, but in either three or six months. By distancing these rewards from the present, their value was no longer seen as immediate, and were then seen as less valuable. The further in the future the reward was to be given, the more likely individuals were to choose to give the reward to their friend, denying themselves of their hypothetical payment. Macaques have not been seen choosing whether to act on impulse or received a delayed reward. However, this is reminiscent of the trade-off between seeking immediate rewards or establishing lengthy, gradually-gratifying relationships with group members seen in macaques. So long as investments in prosociality have a near certain payoff, they will occur. Also, given the recipient's immediate benefits, it may be important to question whether macaques are sensitive to the needs of others, so long as longitudinal benefits are plentiful and reliable. Good givers make good recipients.

Another similar experiment addressed the relationship between altruism and kinship, finding that the surveyed students were willing to decline far greater sums of money for their relatives than for non-relatives of equal social value (Rachlin and Jones, 2008). It is again important to note how the behavior of humans reflects that seen in macaques, as individuals are willing to inflict greater costs upon themselves in order to help relatives than they would for equivalent unrelated affiliates. For macaque socioecologies and human cultures, kinship bears astounding importance.

All in all, it appears that altruism is desirable in humans given certain conditions. As long as costs are not too great, benefits are strong, and the recipients of these benefits are considered valuable individuals, altruism and cooperation will occur (Rachlin and Locey, 2011). In a group that values the services of others, reciprocity becomes a powerful tool. When conditions do not appear reciprocal, they do not seem ideal. Fair reciprocity is often seen as a necessary element for human interaction. That is why individuals who offer to be paid a lower salary are not often hired, as their employers would rather hire a person who values their services (Dufwenberg and Kirchsteiger, 2011). Conversely, it is undesirable to appear to be a freeloader, both for the sake of reputation and continued cooperation. In this way, unlike macaques, humans have much more structured mechanisms for valuing the social work of others, both for the maintenance and upkeep of our social relationships and the preservation of our bank accounts.

It can also be said that research on human altruism has often furthered the idea that altruism is entrenched in human genetic variation. Twin studies indicate that human behavioral tendencies (including altruism and cooperation) are commonly shared between twins (Ebstein et al, 2010). However, such studies often are difficult to reconcile, as adopted twins reared in separate environments are assuredly living in wholly different conditions. Therefore, the environment's input in the variation of these behaviors is often underestimated.

Furthermore, Ebstein cites certain genes as regulating social behavior. However, these genes are often associated with endocrine pathways that would involve chemicals elicited through social interaction. The key here is that these social

interactions are necessary for these pathways to be active. The range of behavioral phenotypic variation is likely an interaction between social environments and highly synergistic, evolved endocrine and neural pathways. Human altruism is not typically seen until the ages of 7 or 8, suggesting a critical period for social behavioral development (Rockenbach et al., 2008). As individuals develop in a given environment, it appears that these tendencies become more likely to become learned and develop via neuroendocrine reward systems.

Human Impacts: From Kanpur to Tourists

The increasingly spreading human population and urbanization of potential spaces for macaques is likely to have effects on the behaviors seen in affected populations. By secluding these individuals and changing their ecological dynamics, humans are dramatically affecting the behavioral repertoires of these groups, resulting in dependencies on humans for basic needs and decreased aggressiveness, as more agreeable macaques have more access to human foods and spaces.

Addressing ecology's role in mediating non-human primate behavior is not only relevant to the study of the origins of altruism and cooperation but also the ecological needs of our often-endangered fellow primates. Observing behavioral anomalies may help elucidate how human behavior may be resulting in populations of abnormal composition that may geographically and behaviorally become more and more dislike in the coming years.

A survey of two tourist locations noted some potential effects of human presence on these populations of macaques (Fuentes et al., 2007). Researchers observed behaviors of both Barbary and rhesus macaques in tourist areas. In these

locations, above normal levels of macaque-human contact, feeding by humans, and human initiated conflicts were observed. As a result, different techniques must be used in order to manage these populations while ensuring their own safety as well as the humans that travel through these areas. In addition to these effects on behavior, this increased contact due to lessened aggression is particularly relevant to health interests. This increased human-macaque contact increases the likelihood that diseases will spread between human and macaque populations.

In such conversations, it is also important to address local human culture's perceptions regarding the presence of monkeys. While the rhesus macaques of Bali have long been incorporated into the mythology of this region, Barbary macaques are considered pests by locals inhabiting Gibraltar, Spain. As a result, macaque dependence on humans for food is more heavily associated with the tourism industry in Gibraltar, as locals are more likely to make sure that their food and food waste is not accessible. In addition to culture, human-macaque interactions and effects are often mediated by policy. One densely populated area in which human-macaque interactions are policed is Singapore, where fines are often given to those who feed macaques and educational programs raise awareness of the effects (primarily health concerns) that result from this contact (Priston and McLennan, 2013). Observers in this area found that rates of macaque feeding by humans were much lower in this city than the aforementioned areas. However, it was noted that feeding was more likely to occur when human children were present.

These cases also reflect the plasticity of macaque behavior. Human presence can remarkably change the behaviors seen in these species. Fuentes et al. conclude by

saying that future primate research should acknowledge the amount of human influence on all studied populations. Humans influence the presence of food and space available for macaques, doing so according to human economic needs as well as conservation policy. By helping to preserve these populations of macaques, humans ensure that their sanctuaries and parks remain natural in a way that is appealing to viewers. While this ensures macaque's food security, it also fosters dependency, behavioral alterations, and increased potential for disease transmission.

Catastrophic effects on social organization have been found in populations of macaques associated with human contact. One such population of bonnet macaques was noted for having relatively small unimale groups, a characteristic that is rarely ever seen in any macaque species (Sinha and Mukhopadhyay, 2013). These bonnet macaques were not closely associated with human systems, such that human food waste was not easily or readily accessible. Macaques living in human settlements did not exhibit these changes in group sex composition, but changes were evident in group size. In determining which ecological factors related to human presence could have driven such social evolution, some researchers have suggested that human food quality and quantity must be addressed. These foods, often nutritionally rich and arriving in uncertain, irregular quantities, create a highly stressed, competitive environment in which only fortunately dominant individuals (like the sole males of the bonnet macaque populations) have access to these high nutrient foods. These changes for these groups have occurred relatively rapidly, resulting in dwindled group size, a highly skewed sex ratio, and biased social reproductive system. With only one

male for such groups, generations of offspring will be highly alike genetically so long as another male does not enter the group.

Social Evolution

In the introduction to this thesis, I questioned the conclusions drawn by many authors that the behaviors seen in macaques are more associated with the evolution of this clade than any environmental factors. In this way, the behavioral differences seen across these species are products of divergent selection pressures that, though ecologically driven, are ultimately reflected in population changes that are manifest in the genetic differences seen across these species.

I suggest that these changes are not simply a product of biological evolution, but also of social evolution. Social systems develop in response to their environment in ways that are profoundly malleable and reactive given differing environments. The anecdotes of human-affected populations are very telling of how macaque social organization and resulting behavior can be altered and magnified by changes in landscape of surrounding resources.

While the divergence seen in these populations is used to justify terms like “egalitarian” and “despotic,” these studies do not address the occasional convergences that are reflected in behavior. By noting any convergences between any unlike populations within and between species, it may be inferred that such behaviors are the product of similar ecological pressures based on similar environments with similar resource availabilities. There may also be social mutations, like new memes. These mutations may be a novel behavior that is started by one individual or a new condition provided by the environment. Regardless of the origin of such a change,

these have multiplicative behavioral consequences that may stereotype and be reflected in the behavior of these groups even after generations have passed. While biological reproduction amounts to the spreading of genes to future populations during occasional breeding cycles, social reproduction regards the repetition of actions between individuals that happens on regular bases. Social evolution is speedy and reactive, occurring in ecological time. As a result, such changes are not reflective of any internal character of individuals as much as they are indicative of a momentary status in a group's social history.

Once one includes environmental inputs in order to demonstrate the diversity of possible behavioral outcomes for groups of given size and composition, it becomes clear that social behavior is primarily a response to varying levels of competition. When competition is present and abundant, aggression results and those who are subordinate are more likely to behave aggressively towards those who have more control over limited resources, sometimes resulting in social reformation (Frank, 2003). Along with this increased aggression comes decreased affiliation: grooming, co-feeding, play behaviors, etc. Conversely, when competitive pressures are minimal, subordinate individuals have more equitable access to resources. As a result, behaving aggressively towards dominant individuals would do more harm to social cohesion, a factor that allows for more evenly distributed resources, than allow further access for subordinates. These individuals inhabit an environment where affiliation is desirable and increases fitness. However, there are instances where behaviors such as these may alter. Groups that prefer social cohesion may become

more prone to social reformation and vice versa given ecological, social, and even seasonal circumstances.

Altruism and Cooperation: The Game is Afoot

In conclusion, I hope that this thesis has addressed contemporary research on altruism, cooperation, and other prosocial tendencies through the lens of macaques. I hope I have been able to fully reflect the limitations of such research and how current interpretations on these behaviors have a tendency to assume genetic evolution as a primary driver of the evolution of sociality and cooperation. Speciation is not entirely a matter of genes. It also often involves changes in behavior, changes in resource needs and interactions with the environment, or changes in location. Furthermore, these changes are not mutually exclusive, as changes in the environment are duly met with changes in social pressures and selective pressures which result in changes in behavior. This does not mean that every new behavior is a formulated and fitting response to changing surroundings; there is a certain level of random innovation inherent to living in a social system. It is important to distinguish minute phenomena from broader trends in behavioral changes and their extended relationship with social organization. The more constrained conditions become, the more competitive behavior becomes, resulting in (oftentimes sudden) decreases in altruism and cooperation.

Furthermore, I hope that this thesis calls into question the role of humans in interacting with the macaques described here. As human endeavors change the conditions of habitats for non-human primates as well as all living creatures, it seems likely that behaviors are continually responding to change at a faster pace than

genetics can. This can result in increased pressures when animals live in smaller, divided territories with less abundant resources. This also may result in decreased pressures, as humans have created spaces where animals can thrive and depend upon human waste. Humans will certainly continue to play a role in managing the spaces of this planet, and it is crucial to recognize where and when behaviors change, as these may be preliminary warnings that populations are vulnerable. Of the 22 extant macaque species, 19 have been noted for their decreasing populations (IUCN, 2014). Like in times of peril in human societies, macaques may not react well to these dangers. The survival of the group may diminish in importance while the survival of the individual grows mightier in its influence. By protecting these areas and ensuring the survival of primates, the behaviors seen may find a healthier medium between these two survival and social instincts.

This study is also important to understanding human behavior. Why are humans so profoundly capable of kind deeds? We are often rewarded for doing them, as our reputations, friendships, and even our bodies are rewarded by our actions. Sometimes, selfishness may be altogether absent, as there truly are no explicable gains. This does not mean that the ability and tendency is maladaptive. As long as these inclinations are met with net gain, they will be upheld. If a person were to hand a few dollars to a homeless individual on the street, they are not going to expect anything in return. Perhaps it makes them feel good to do so, or the recipient reminds them of someone they know, strengthening their sympathy. Regardless, these actions are not planned with any hope of reward. Assuming the actions of macaques are somehow different, solely based on a need to self-replicate, ignores the possibility

that these behaviors can be generalized such that individual altruistic acts may not bear net gains. Being an altruist for years is adaptive and increases fitness; being an altruist once or twice is less so. There is more to these behaviors than genetics or even its interaction with the environment can explain. By incorporating the ecology of social groups, their histories, and their evolution, a more complete view of social behavior's divergent capabilities can be understood, both at the level of the individual and that of the group. The gene may be selfish, and the individual's behaviors may often be so as well. However, isolated groups do not always operate on competition, such that selfishness is not as feasible at this larger scale.

Let's return to the *Altruism Game* one last time. The players have become quite disgruntled, as their initial card draws have realized that the game is unfair. The players refuse to continue playing, as they have slowly realized how convoluted the system is. They mutually agree to stop playing. Within the confines of a game defined by reciprocity, cooperative competition, and a desire to have the highest score, they have failed. But by recognizing how the system has failed the group at the expense of the individual, they have won the *Altruism Game*. Due to a technicality mentioned in the rules in Chapter 1, those who do not finish the game to its completion citing the game's inherent imbalance and flaws are actually the most successfully cooperative, such that all players win. While this would make for a terribly unpopular board game or competition of any kind, it demonstrates the fact that seemingly cooperative pursuits are not without their competitive elements. If competitive constraints were completely removed or at the very least reduced, perhaps more examples of altruism and cooperation would be observed in both humans and macaques. By promoting the

welfare of all individuals and reducing competitive constraints, it seems possible that cooperation may be more commonly observed. In such an idyllic environment, altruism and cooperation may become further removed from explanations based on underpinning selfishness.

When I was young, the words of the golden rule, “treat others the way you would want to be treated” or some variation on this line, were often repeated to me by teachers and classroom posters. At its core is a slightly egocentric appeal: one should behave nicely towards others because this would promote an environment in which they would behave nicely towards oneself. However, it also encourages a motive for kindness, as knowledge of one’s own needs fosters an understanding of the needs of other individuals, as they may be similar to one’s own. It appears that socio-ecological variation must be examined in order to understand the nature of selfish and (potentially) selfless altruism. Macaques may scratch an affiliate’s back hoping to be scratched in return. However, this reward is not necessary in contexts of low competition and high social cohesion, precluding groups that would prefer social maintenance over social reformation. We cannot easily assume an intention. Individuals in low-competitive environments may be doing so, recalling that having their own back scratched feels good. Or, better yet, realizing that their friends enjoy having their back scratched.

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