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"Cooperation in Japanese Macaques (*Macaca fuscata*)"

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Ryan Sigmundson

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When one considers the history of humankind, it can seem little more than the history of a string of conflicts. One might conclude from this appearance that humans are a particularly non-cooperative species with little concern for the well-being of others, but viewed within the context of the animal kingdom as a whole it quickly becomes apparent that quite the opposite is the case. Humans engage in cooperative and prosocial behavior to an unusual extent, certainly more so than any other primate species thus far examined (Burkart et al., 2014). The relative infrequency of such behaviors should not surprise anyone familiar with the evolutionary bias towards inheritance of "selfish" traits. An individual inclined towards cooperative and prosocial behaviors is left open to potential exploitation by others and will consequently be less likely to pass its genes into future generations, putting an end to the genetic line that facilitated that behavior. This flips the question into not why animals help each other so infrequently, but why they help each other in the first place.

The answer to why cooperation occurs at all varies depending on the particulars of the case. In "mutualisms", the individuals involved both receive immediate payoffs from their actions. This class of interaction can be easily explained by each individual acting in favor of their own immediate interests. The cases of cooperation requiring explanation are those in which there is a degree of payoff uncertainty involved for either of the cooperating individuals. Defection of one individual may result in a loss of reward for the cooperative individual while providing a fitness advantage for the uncooperative individual. The mechanisms proposed to account for the evolution of prosocial behaviors such as cooperation are inclusive fitness (Hamilton, 1964) and reciprocal altruism (Trivers, 1971). Inclusive fitness theory addresses cases where a relative is the recipient of a prosocial action. The action need not directly benefit the acting individual because the action still results in an indirect fitness gain through the genetic material that they share with their relative. In reciprocal altruism, an individual receives direct benefits from their action from the recipient of the immediate payoffs, but at a time temporally removed from the initial payoff period.

Cooperation has been studied experimentally in species as diverse as elephants (*Elephas maximus*; Plotnik, Lair, Suphachoksahakun, & de Waal, 2011), hyenas (*Crocuta crocuta*; Drea & Carter, 2009), dolphins (*Tursiops truncatus*; Jaakola, Guarino, Donegan, & King, 2018), wolves (*Canis lupus*; Marshall-Pescini, Schwarz, Kostelnik, Virányi, & Range, 2017), keas (*Nestor notabilis*; Schwing, Jocteur, Wein, Noë, & Massen, 2016), ravens (*Corvus corax*; Massen, Ritter, & Bugnyar, 2015), and a variety of primate species (Chalmeau & Gallo, 1996; Chalmeau, Lardeux, Brandibas, & Gallo, 1997; Mendres & de

Waal, 2000; Cronin, Kurian, & Snowdon, 2005; Molesti & Majolo, 2016). Many of these studies have made use of variations of the string pulling task first pioneered by Crawford (1937) and later modified into the loose string paradigm (Hirata, 2003). In the basic form of this paradigm, two individuals must simultaneously pull opposite ends of a rope attached to a platform bearing food rewards in order to pull it closer and obtain their reward.

One of the immediate difficulties in investigating cooperation in non-human animals pertains to a more general problem in the study of animal behavior: inferring what is going on in the mind of the animals involved. Whether or not two animals engaging in joint action to achieve a shared goal can be classified as cooperating depends on the specifics of the situation and the definition of cooperation used. Unless proper steps are taken in experimental design, one cannot always infer whether the animals involved in the experiment had any understanding of the task, let alone the role that their partner played in it. Without the presence of understanding in the animals involved, any apparent cooperations that may have occurred could have been entirely coincidental–two individuals acting independently toward the same goal at the same time without any real grasp of the nature of the task. Only the broadest of definitions would classify such a case as an instance of cooperation. Before issues of cognition can be addressed, researchers must first decide what exactly they mean when they use the term "cooperation" and clarify how this definition can be applied to the behavior of animals.

1.1 Defining Cooperation

The term "cooperation" has been subject to a multitude of usages, impeding discussion of the subject between, and sometimes even within, fields. Specifics of the definition have varied considerably, but the key difference between definitions lays in whether cooperation is defined according to its form or according to its outcomes. The primatologists Boesch and Boesch (1989), for example, define cooperative hunting purely in terms of the form that it takes while making no mention of the outcomes and reward divisions that may occur as a result. In contrast, the economists Bowles and Gintis (2003) define cooperation in terms of its costs and benefits, placing the focus of the definition on its resultant outcome rather than the action itself. Outcome-based definitions have the advantage of being more readily quantifiable, but are problematic in that they overlook cases of unsuccessful goal-oriented joint action.

In an attempt to reduce the terminological confusion surrounding "cooperation", Noë (2006) proposed to define cooperation as, "all interactions or series of interactions that, as a rule (or 'on average'), result in a net gain for all participants". One advantage of using this definition is that it does not define cooperation in terms of its outcome for the participants in any particular instance. This way, if two individuals perform a task together that results in the acquisition of food but one of the individuals monopolizes the food source and gives none to their partner, the action can still be said to have been cooperative. A tendency toward cooperative behavior in a species can become an evolutionarily stable strategy as long as it *on average* provides a fitness advantage to the cooperating individuals, and that fitness advantage need not take the form of direct gains. In my example of food source monopolization, the individual who received no food may still benefit indirectly by forming or maintaining a social bond with a dominant individual in their social group.

It should be noted that Noë (2006)'s definition of cooperation makes no mention of the cognitive abilities that may contribute to cooperative actions. The cooperating individuals need not possess any understanding of the necessity of their partner or the role that they play. The cooperating agents could very well be plants rather than intentional agents and still fit into the definition just as clearly. This isn't necessarily problematic, but as I'm interested in the cognitions contributing to cooperative actions, modifications of this basic definition are required to capture the level of understanding involved in solving a cooperative task.

Boesch and Boesch (1989) studied group hunting in a wild population of chimpanzees (*Pan troglodytes*). Chimpanzees regularly engage in group hunts and a goal of the authors was to examine the level of coordination involved in these hunts and whether they can rightfully be classified as instances of deliberate cooperation. To clarify the level of organization involved in a cooperative hunt, the authors proposed a four-level system of increasing complexity. The first level, "similarity", involves the hunters performing the same action directed toward the same prey, but without any spatial or temporal coordination. At the second level, "synchrony", participating hunters coordinate similar actions with the same target temporally but not spatially. "Coordination", the third level of organization, adds spatial coordination to the previous level. At the final level, "collaboration", hunters direct different but complementary actions toward the same prey.

The significance of these four levels is that they have different cognitive requirements in understanding the role that cooperative partners are playing in one's own activity. While joint actions at the "similarity" level can be explained by two or more individuals acting independently of one another with regard to the same eliciting stimulus and thereby giving

the appearance of cooperation, the adoption of complementary actions at the "collaboration" level requires understanding not only of another individual's involvement in one's own activity, but of the particular role that those partners are adopting and how they can be complemented by one's own actions. An important feature of Boesch and Boesch (1989)'s divisions is that they have been formulated in such a way as to have objective, potentially quantifiable outputs from which one can infer cognition. This renders them both theoretically and practically useful.

Any useful definition of cooperation from the cognitive perspective needs to be able to discriminate between simultaneous action giving the appearance of cooperation but lacking any intent on the part of the cooperators and deliberate cooperation rooting from an understanding of the role that the partner has played in the action. For the purposes of this thesis, I will be using Noë (2006)'s definition of cooperation informed by the framework of cooperative activity outlined by Boesch and Boesch (1989) to identify classes of actions associated with different cognitions and levels of intentionality on the part of the cooperating individuals. Such a definition is advantageous in that it can be applied directly to animal behavior, using directly observable outcomes to infer the presence of the cognitive abilities minimally necessary to produce such outcomes. It further serves to inform experimental design by delimiting the features that must necessarily be present in order to discriminate true cooperation from superficially similar cases.

1.2 Cognitive Components of Cooperation

Cognitions that we take for granted may not always be present in non-human species. Recognizing other individuals and remembering the outcome of past interactions with them, the ability to infer the mental state and intention of others, the ability to understand complementary roles in a task and adopt the appropriate role in a given situation, and the basic ability to coordinate one's actions in time and space with that of another are all cognitive capacities whose presence may constrain a species' potential to engage in cooperative activity.

In order to infer the cognitions of non-human animals, it is necessary to work backward from their actions. Often there will be many possible explanations as to why an individual behaved the way that it did in any particular instance, so experiments need to be painstakingly designed to investigate many different possible explanations until a clear best fit can be found to the data. Demonstrating that two individuals cooperated with one another to achieve a particular goal requires setting up an experiment in such a way as to provide

evidence against the alternative explanation–that is, that the observed cooperative action was entirely coincidental. Negative findings can just as readily indicate a poorly designed experiment as a lack of potential in a species. Once it has been established that a species is capable of deliberate cooperation, one still needs to address why cooperation occurs in some instances but not others. Factors such as reward equity, partner choice, and reciprocity may contribute to an individual's decision to cooperate, and only well-designed experiments can succeed in teasing apart whether and under what conditions they may contribute.

Building on the four levels of cooperative activity proposed by Boesch and Boesch (1989), Chalmeau and Gallo (1996) reformulated their framework into three readily testable levels and devised an experimental setup capable of discriminating between those levels so as to assess the level of understanding of the individuals involved. Their experiment required two individuals to simultaneously pull two handles to receive food rewards. At the first level of understanding, individuals operate the device whenever food is placed on the platform independent of the presence of any potential cooperative partner. This may still lead to success if another individual pursues the same strategy at the other handle at the same time, but it indicates only a basic understanding that operating the device can lead to food acquisition. At the second level of understanding, individuals operate the device when a partner is present at the handle. This indicates an understanding that a partner is necessary if one is to successfully operate the device. At the third level of understanding, individuals operate the device in such a way as to line up their actions with the actions of their partner. In other words, they understand the specific action required of their partner and the need to coordinate their own action with that action. This level of understanding is indicated behaviorally not only by specificity of device operation, but by individuals actively seeking information about their partner's position and actions (as determined by frequency and target of looking behavior). Chalmeau and Gallo (1996) went on to demonstrate the presence of this third level of understanding in a pair of chimpanzees, one of which increased its rate of glancing directed at his cooperative partner as well as apparent behavioral coordination over the course of their cooperation experiment. In a further study, Chalmeau, Lardeux, Brandibas, and Gallo (1997) demonstrated the presence of similar capacities in orangutans (*Pongo pygmaeus*), with one member of the cooperative pair showing improvements in glancing behaviors and behavioral coordination over the course of the experiment.

In applying the experimental setup of Chalmeau and Gallo (1996) to capuchin monkeys (*Cebus apella*), Chalmeau, Visalberghi, Berghi, and Gallo (1997) concluded that

though the capuchins were successful at the task, they had no understanding of the role that their partner played in their success. The level of cooperation in capuchin monkeys observed by the authors corresponded only to the "similarity" level of Boesch and Boesch (1989), in which two individuals perform the same action directed toward the same goal at the same time. No genuine coordination between the partners was demonstrable and the authors could only conclude that the successes of the capuchins were entirely coincidental. Follow-up studies conducted by Visalberghi (1997) and Visalberghi, Quarantotti, and Tranchida (2000) again found that capuchins are not sensitive to the behavior of their partner in the task and are at best minimally sensitive to the spatial positioning of their partner.

Mendres and de Waal (2000) made use of a different cooperative task than previous studies with the goal of making the experimental apparatus more intuitive for capuchin monkeys. Contrary to previous findings, they determined that capuchins are sensitive to the presence of a cooperative partner and they do visually monitor them. They concluded that the findings of Chalmeau, Visalberghi, et al. (1997) were artefacts of the experimental setup they had chosen for use in their investigation. Their study serves to highlight the importance of selecting an intuitive task for the species under study, as seemingly minor differences in experimental setup can yield entirely different results.

Further studies using capuchins have examined the specific factors that influence the decision whether to cooperate. For example, rate of successful cooperation was lower when only one food reward was provided to the cooperating individuals (de Waal & Berger, 2000). In cases where multiple food rewards were provided, individuals were less likely to cooperate when the rewards were clumped together at a single location rather than distributed. This effect is sensitive to kinship and dominance factors, such that only lower-ranking individuals paired with non-kin will lower their rate of pulling, presumably because their cooperative partner would monopolize the food source under these conditions (de Waal & Davis, 2003).

Does something akin to fairness come into play during reward distributions following cooperative interactions, and, if so, what cognitive mechanisms govern those distributions? Hauser, Chen, Chan, and Huang (2003) investigated food sharing in unrelated cotton-top tamarins and determined that not only do tamarins distinguish between receiving food as the result of an altruistic action and receiving food as the byproduct of a selfish act, they are more likely to reciprocate food exchange in the case of the altruistic individual. This demonstrates a clear behavioral tendency in the species to "pay back" individuals who have provided help in the past. Likewise, chimpanzees have been shown to react to the perceived trustworthiness of their partner in a trust game by adjusting their future play with that partner (Engelmann,

Herrmann, & Tomasello, 2015), while blue jays (*Cyanocitta cristata*) have been shown to be most likely to cooperate in an iterated prisoner's dilemma after mutual cooperation in the previous round (Stephens, McLinn, & Stevens, 2002). Under naturalistic conditions, Krams, Krama, Iguane, and Mänd (2008) demonstrated that the pied flycatcher (*Ficedula hypoleuca*) will selectively take part in cooperative mobbing with neighbors that helped them in the past. In an experiment examining cooperative behavior in ravens using the loose string paradigm, Massen, Ritter, and Bugnyar (2015) concluded that subsequent cooperation is more likely to occur within a dyad if their previous interaction resulted in equal reward division. Taken together, these results suggest that a sensitivity to fairness exists in some parts of the animal kingdom, at least insofar as it means refraining from cooperating with partners who have defected in the past.

The mechanism underlying this reciprocation may take some form of symmetry-based reciprocity, in which individuals direct help preferentially towards close associates, and due to the symmetrical nature of their relationship, it appears that they are paying one another back for past assistance. Alternatively, it may take the form of calculated reciprocity, in which favors are explicitly tracked and reciprocated accordingly (de Waal & Luttrell, 1988). Though the second possibility likely imposes a higher cognitive load on individuals than the first, the two mechanisms may result in behavioral output that appears identical if cares are not taken to tease them apart. The key difference between the behavioral outputs of the two mechanisms is that in the case of calculated reciprocity, an individual's likelihood of providing help to a conspecific should increase after that conspecific has helped them, while with symmetry-based reciprocity the likelihood of helping that conspecific should remain more or less stable regardless of any recently received favors. In an experiment designed to tease these mechanisms apart in capuchins, de Waal (2000) concluded that they were using what he terms "attitudinal reciprocity", in which an individual mirrors the behavior of the other towards oneself, essentially developing an attitude towards them that guides their future interactions. In his study, this meant that if the first capuchin to receive food tolerated food collection by the second capuchin, that monkey will be more likely to tolerate food collection by the first when their positions are reversed.

Further developing this line of argumentation, Schino and Aureli (2009) suggest that a system of emotional bookkeeping is the mechanism underlying primate reciprocity. Grooming, agonistic support, tolerance, and food sharing are the low-cost other-directed actions most commonly exchanged, and emotional disposition constitutes the medium that these actions are exchanged for. This has payoffs in the realm of partner choice in the future,

in which individuals select their collaborators on the basis of their emotional disposition towards that potential partner. Rather than calculating potential future returns from a given costly other-directed action, individuals are acting based on past positive interactions in a general sense. Animal friendship research lends support to this model with the intuitive finding that animals who have formed close social bonds with one another are more likely to work together in the future, direct stress-reducing affiliative behaviors such as grooming towards one another, and provide support for one another during conflicts (Massen, Sterck, & de Vos, 2010). This type of reciprocity is less cognitively demanding than calculated forms of reciprocity, requiring only a memory of individual identity and the ability to maintain a reactive emotional disposition toward that individual rather than any sort of episodic memory recording individual interactions.

Moving beyond the cognitive components of cooperation, the social organization of a species can serve to place constraints upon the display of cooperative behavior in a species. If a species does not generally live in groups, possessing the cognitive capacities to engage in cooperation may not be enough to overcome limitations in the social capabilities of the species. Even within group-living species, social tolerance on both the group- and dyad-level varies considerably and may impede the display of cooperative behavior. Cooperation is inherently social in nature, and, as such, the social environment of a species determines the conditions under which it may emerge.

1.3 Social Tolerance and Cooperation

A low level of social tolerance between individuals that could potentially serve as cooperative partners may inhibit the display of cooperative behavior even if those particular individuals are cognitively capable of cooperating. The tolerance hypothesis posits that a higher level of tolerance between two individuals will increase the likelihood that those individuals will succeed in solving a novel task requiring joint effort. Melis, Hare, and Tomasello (2006a) explicitly tested this prediction in a series of experiments involving chimpanzees. They found that chimpanzees with a higher level of tolerance toward one another were more likely to solve the cooperative task together. Furthermore, when previously successful individuals had their partner swapped out for a less tolerant individual, they were no longer successful in solving the task, while previously unsuccessful individuals were more likely to succeed after their partner was swapped for a more tolerant partner. This demonstrates that success within a cooperative task isn't just a function of the ability of the individuals involved, but of the social tolerance present within that particular dyad.

On the level of the species as a whole, the idea of social tolerance constraints on cooperation can be extended to explain cross-species differences in cooperative behavior. A low level of social tolerance within a species could inhibit the display of cooperative behavior even if that species is cognitively capable of performing cooperative tasks. For this reason, much of the early experimental research into cooperation (outlined in the previous section) focused on capuchins, a species of New World monkey with a high level of social tolerance.

The high social tolerance found within callitrichid primates makes them another attractive group in which to investigate cooperation. Common marmosets (*Callithrix jacchus*) have been demonstrated to have a high rate of cooperation, though the overall pattern of cooperation was affected by the rank relationships of the different dyads (Werdenich & Huber, 2002). Cronin, Kurian, and Snowdon (2005) investigated cooperative behavior in tamarins (*Saguinus oedipus*) using an apparatus that provided both monkeys with a reward via sliding trays upon successful cooperation. The authors concluded that tamarins are aware of the role that their partner plays in the experiment and can coordinate their actions accordingly. Interestingly, the tamarins showed a higher rate of task efficiency than previous studies had demonstrated using great apes.

If social tolerance within a species is a large determinant of their tendency to engage in cooperative action, closely related species that differ in social tolerance should cooperate in accordance with this social tolerance gradient. The species within genus *Macaca* are behaviorally widely dispersed with regard to social tolerance (Thierry, 2000), making them suitable models to examine the effect of social tolerance on cooperation. A study comparing Tonkean macaques (*Macaca tonkeana*) and rhesus macaques (*M. mulatta*) on a cooperative task found that cooperation was almost completely absent in rhesus macaques, the less tolerant of the two, while it occurred frequently in the more tolerant species (Petit, Desportes, & Thierry, 1992). That being said, there was no sign of active behavioral coordination in either species and the successful cooperative actions that occurred were likely due to chance. In a study involving Japanese macaques (*M. fuscata*), one of the least socially tolerant species within genus *Macaca*, the authors failed to observe any spontaneous cooperative behavior within the group (Burton, 1977), which may be attributable to the low level of tolerance within the species.

A more recent study of cooperation in Japanese macaques revisited their capacity to engage in cooperative behaviors and demonstrated that they are capable of such interactions, but this capacity is heavily mediated by inter-group variation in cooperation. Kaigaishi, Nakamichi, and Yamada (2019) conducted a form of the loose string paradigm with two

different groups of Japanese macaques known to vary drastically in their level of within-group social tolerance. The more socially tolerant of the two groups succeeded in cooperating to obtain food at a very high rate while the less socially tolerant of the groups achieved only a few isolated instances of successful cooperation. This study illustrates that social tolerance impacts the expression of cooperative behavior not only at the level of dyad and species, but between groups within a species as well.

To effectively investigate social factors such as tolerance in a species, study needs to take place in an intact social environment. Ideally, this means conducting research under naturalistic conditions. Practical constraints imposed by these conditions introduce obstacles in experimental design along with associated difficulties in the interpretation of results (for a review, see: Cronin, Jacobson, Bonnie, & Hopper, 2017). There is a tradeoff between the control that can be achieved under artificial conditions and the ecological validity that can be acquired through investigation in natural settings. Active manipulation is not always possible under these conditions, and for practical reasons studies seeking to examine social factors in an authentic social environment often fall somewhere between the two extremes. Nevertheless, such studies are essential to achieve an understanding of the influence of social environment upon animal behavior.

1.4 Cooperation Under Naturalistic Conditions

Observational studies of cooperative behavior under naturalistic conditions have occasionally been carried out (Boesch & Boesch, 1989; Rose, 1997), but studies where cooperation has been investigated experimentally under naturalistic conditions are the exception rather than the norm. Though investigating cooperation under more contrived conditions can serve to tell us whether a species is cognitively capable of cooperation, it cannot tell us whether a species *will* cooperate within its ecological context. Observational studies may provide good evidence for this, but the fact of the matter is that in an observational study one cannot as easily tease apart all of the factors leading to the observed behavior. This renders it much more difficult to determine whether an observed set of actions qualify as cooperation, not to mention the animals under observation may simply never encounter a situation that would require them to engage in cooperation over the observational period. Particularly in cases where the behavior of interest is under emotional regulation, as is likely the case with social behaviors such as cooperation, collection of physiological information may be required to test hypotheses (Massen, Berens, Martin, Stocker, & Brosnan, 2019). This information can be difficult or impossible to obtain under naturalistic

conditions, amplifying the need to find a creative middle ground between experimental and natural settings. Using the two approaches in combination can be effective, as can conducting experiments under naturalistic or semi-naturalistic conditions. In this case, experimental manipulation can be actively carried out while still maintaining a high degree of ecological validity.

A major reason why conducting cooperation experiments under natural conditions is so essential is that cooperation is at its core a social endeavor. In typical cooperation studies, two individuals are isolated from their social group and given the opportunity to cooperate with one another. This removes them from their social context, eliminating the effects of what are in some species ever-present factors such as dominance hierarchies, familial relationships, and social bonds. The effect of this is especially pronounced the more gregarious a given species is in its natural environment, with a heightened stress response following separation being a very real possibility (Cronin et al., 2017). Furthermore, such experiments effectively remove the element of partner choice from the individual. Chimpanzees, for example, have been demonstrated to actively seek out and recruit the best cooperative partner based on their previous interactions when given the opportunity (Melis, Hare, & Tomasello, 2006b). A second cooperation experiment designed to examine partner preference in chimpanzees, this time conducted in a large enclosure with all individuals selected for the experiment simultaneously present, found that chimpanzees preferentially approached the experimental apparatus when a preferred partner was present (Suchak, Eppley, Campbell, & de Waal, 2014). Preferred partners in their experiment proved to be kin or individuals with a similar rank, both of which are ever-present components of the chimpanzee's social environment that are often removed in more structured experimental settings. An experiment using the string-pull paradigm with ravens found that they preferentially cooperate with close affiliates, but went on to challenge whether this preference was due to relationship quality itself or merely mediated by tolerance for spatial proximity (Asakawa-Haas, Schiestl, Bugnyar, & Massen, 2016). These experiments serve to underscore the necessity of embedding experiments within the typical social context of the species, at least insofar as the behaviors under examination are social in nature.

Beyond the impact of neglecting social context, the animals generally used in cooperation studies have been raised in captivity and have had a high level of interaction with humans, which in itself can lead to the development of species-atypical behaviors (in the case of referential pointing in orangutans, for example: Call & Tomasello, 1994). Moreover, the ontogenetic development of cognitive domains varies in accordance with an individual's

upbringing conditions, which can result in cognitive profiles in captive populations that are not reflective of their capabilities when brought up in a species-typical environment (Boesch, 2007). Though studies making use of these populations still represent valid demonstrations of cognitive capacities within a species, the possibility of species-atypical behaviors and cognitive profiles within such populations calls into question the applicability of their findings to naturally occurring groups of the species.

A notable exception to the general dearth of experimental cooperation studies under naturalistic conditions was conducted by Molesti and Majolo (2016). They examined Barbary macaques (*M. sylvanus*), a relatively socially tolerant species of macaques, in a cooperative task taking place in a naturalistic setting. They observed a high rate of cooperation in this species, particularly amongst dyads with a higher level of social tolerance. Furthermore, their experimental apparatus rendered coincidental instances of cooperation unlikely to occur, suggesting that the individuals involved had some understanding of their partner's role in the task.

The Japanese macaque study discussed in the previous section (Kaigaishi, Nakamichi, & Yamada, 2019) was also conducted under naturalistic conditions. Their most successful dyads were composed of individuals from the same matriline, so partner choice likely played a role in the outcome of their experiment. It was the combination of structured experiment within a social context allowing for free partner choice that allowed for the expression of a cooperative capacity that could have been otherwise overlooked, as it was in Burton (1977)'s previous exploration of cooperative behavior in Japanese macaques.

1.5 The Interdisciplinary Approach

Any endeavor attempting to bridge the gap between animal behavior and animal cognition needs in its toolbox the experimental techniques of the empiricists, the conceptual framework of the cognitivists, and the explanatory power of evolutionary theory. On their own, experimental results can offer only a limited explanation of an observed phenomena. Synthesizing those results with the mentalistic concepts and terminology of the cognitivists renders it possible to draw conclusions about the mental constructs that promote and maintain these behaviors. Situating these conclusions within the evolutionary framework allows for speculation as to how the mechanisms promoting these behaviors may have developed and changed over the course of evolution.

No single field can present a complete picture when it comes to a topic as complex as the inner workings of the mind. In the later discussion of my results, conceptual approaches

with their roots in philosophy of mind and cognitive psychology will be brought to bear on the interpretation of my thesis. This will shed light upon what may be going on in the mind of these primates during the experiment. In the tradition of comparative psychology, these results will be compared and contrasted with the abilities of humans as well as non-human animals to contribute to unravelling the rich tapestry that is our evolutionary history.

1.6 The Present Study

This thesis examines cooperative behavior in Japanese macaques using an experiment conducted under semi-naturalistic conditions so as to allow free partner choice to occur amongst the participating individuals. The study population consisted of 164 individuals housed in a 40,000 m^2 enclosure originally established for the purpose of tourism. An apparatus requiring two individuals to synchronize their pulling behavior in order to receive a food reward was set up in an open-air hut within the macaque enclosure. Sessions consisting of 10 trials were run on a daily basis and all participating individuals were recorded along with any potential partners present in the surrounding area. Two pieces of food were loaded into the apparatus during all sessions to examine reward division following successful dyadic cooperation. Upon successful operation of the apparatus, the food rewards were released onto a platform in the center of the hut. Releasing the rewards to the center of the hut rather than directly providing them to the participating individuals rendered the rewards susceptible to monopolization and thievery–possibilities that are ever-present in the social environment of Japanese macaques. All monkeys within the group were free to approach the device at any time, whether to manipulate the apparatus, attempt to steal food from successful individuals, or merely observe. Maintenance of these social factors granted a high level of ecological validity to the experiment.

Given that the capacity to succeed in cooperative tasks has been previously demonstrated in this species, but the same study concluded that expression of this capacity varies between groups presumably due to variance in social tolerance at the group level (Kaigaishi, Nakamichi, Yamada, 2019), the first goal of this experiment was to examine whether cooperative behavior is prevalent within this particular group of Japanese macaques. Accordingly, I predicted that the monkeys in my experimental group would become increasingly proficient at dyadic operation of the apparatus over the course of the experiment. This would be evidenced by an increase in the relative frequency of successful attempts at operating the apparatus.

The next goal of this experiment was to examine whether the monkeys possess an understanding of the task that they are performing and recognize the role that their partner played in their own success. This would be reflected as an increase in their likelihood to make attempts at operating the apparatus in the presence of a potential partner. This likelihood may show specificity to the presence of particular partners that they prefer to cooperate with. In the absence of a partner, I predicted an increase in their likelihood to display waiting behaviors, defined as a suppression of apparatus manipulation while remaining in the area until such a time that a potential partner arrives.

Following the reasoning of inclusive fitness theory, kin should be more likely to cooperate with one another and more forgiving of reward division inequity following cooperation. These instances of cooperation between kin should be facilitated by the higher level of social tolerance between those individuals. One aim of this study was to examine whether kin were more likely to cooperate with one another than with non-kin. In addition, I compared the frequency of reward division inequity between kin and non-kin dyads.

The foremost strength of this study lays in its implementation of an experimental paradigm within an intact social environment. The importance of social dynamics in regulating the expression of cooperative capacities, particularly in socially intolerant group-living species such as Japanese macaques, cannot be understated. This study will contribute to the ongoing conversation regarding cooperative behavior throughout the animal kingdom while helping to shed light upon the underlying proximate mechanisms that govern it.

Methodology

2.1 Subjects

The experimental sample was obtained from a population of Japanese macaques (*Macaca fuscata*) living under semi-natural conditions at the Affenberg Landskron, Carinthia, Austria in a 40,000 m^2 enclosure. The Affenberg Landskron population originates from a group of Japanese macaques, and was introduced to the area in 1996 after being taken from Minoo City, Japan. The majority of the macaques presently living in the area were born on location and have spent their entire life there. At the beginning of data collection, the enclosure contained 164 individuals living in a single group. The population consisted of 79 adult females (>3.5 years of age), 51 adult males (>4.5 years of age), 24 juveniles, and 10 infants. The proportion of adult males in the group is higher than one would expect under natural conditions, but should not have affected my results as few of them participated in the experiment. The animal care staff of Affenberg Landskron provides food for the macaques once or twice a day (either splitting the same amount of food between two feedings or delivering it all at once) with the first feeding occurring between 0900h and 1100h. Provisioned food consists of various fruits and vegetables, as well as wheat. The natural vegetation of the area provides the monkeys with additional foraging opportunities. Testing occurred between regular feeding sessions and did not involve subjecting the macaques to deprivation states. Water is available ad libitum at any time through multiple drinking stations as well as a natural stream that goes through the enclosure.

The macaques participating in the experiment were accustomed to the presence of humans due to regular interaction with keepers, researchers, and tourists. Tourists are allowed into the enclosure on guided tours running from the beginning of April until the end of October, though physical interactions with monkeys are prohibited. As data collection occurred between October and April, only a portion of the training phase occurred during a period with regular visitors in the park. Guided tours take place in only a restricted part of the enclosure that does not include the research hut where the experiment was conducted.

Participation in our experiments was on a voluntary basis; i.e., participants were not actively selected, nor separated from the group, and participation varied by session depending on which members of the population took an interest in the experiment during that particular session. Accordingly, group size in the experimental area during testing sessions varied considerably across sessions. In sum, data were collected on an opportunistic basis.

2.2 Apparatus

The apparatus used to measure cooperation was a version of the string pulling paradigm pioneered by Crawford (1937) and later modified into the loose string paradigm by Hirata (2003). In these paradigms, two individuals have an opportunity to obtain food through cooperation. The desired food is placed out of reach and can only be obtained through

simultaneously pulling two separate rope ends that have been placed too far apart for any one individual to reach alone. Variations of this paradigm have been tested on many animal species including primates (Mendres & de Waal, 2000; Halsey, Bezerra, & Souto, 2006; Molesti & Majolo, 2016), corvids (Massen, Ritter, & Bugnyar, 2015; Scheid & Noë, 2010), canines (Marshall-Pescini, Schwarz, Kostelnik, Virányi, & Range, 2017), and even insects (Alem et al., 2016). A key difference between the apparatus used in my own study and those used in typical cooperation studies is that while typical string pulling setups involve the participants pulling food towards them, my apparatus releases food at a fixed point approximately 1 meter from either pulling individual following successful operation of the apparatus. Such a setup provides the advantage of allowing for better observation of the effects of food sharing, food source monopolization, and food theft by individuals involved but also those uninvolved in the cooperative action. A notable disadvantage of my setup is the comparative lack of visual feedback provided to the pulling individuals during manipulation of the apparatus.

The body of the apparatus was essentially a wooden platform with a clear lockbox mounted on top in which food could be placed (Figure 1). A copper pipe that housed a wire ending in a loop extended from two opposite sides of the lockbox to an area in front of the apparatus. Each loop could be pulled to release one of the two pins within the lockbox (Figure 2). The floor of the lockbox consisted of a trapdoor mechanism that would drop open when both pins holding it in place were released. The experimenter was able to place food in the lockbox through a door in the top, but the only way for the monkeys to access the food was to spring the trap door by pulling both loops simultaneously. Successful release of the trapdoor resulted in the enclosed food being dropped onto the wooden platform below. The platform could be approached from all directions, which allowed for better observation of the impact of social dynamics on reward division. During the experimental phase, the loops were positioned two meters apart so that no single individual could reach both loops simultaneously. The training phase, the rationale of which will be explained in the next section, positioned the loops only 20 centimeters apart (Figure 3).

Figure 1. In the experimental setup, the loops were positioned 2m apart so that coordinated pulling was necessary to acquire food.

Figure 2. The pin-based mechanism holding the trapdoor closed. The left pin is shown in the closed position while the right is in the open position. When both are open, the trapdoor drops down releasing the contents of the compartment. The spring serves to return both pins to the closed position after each pull.

Figure 3. In the training setup, the loops were positioned 20 cm apart so that an individual is capable of reaching both loops. During Phase I, only pulling a single loop was required to release the food, while in Phase II, pulling both loops simultaneously was required.

Figure 4. A wooden hut within the enclosure housed the cooperation experiment. The open doorframes in each corner allowed the monkeys to enter and leave the hut at any time.

The apparatus was housed in a wooden hut within the enclosure that had been built for the purpose of research (Figure 4). There was an open doorframe located at each corner of the hut to allow individuals to enter and leave the area at will. The monkeys had already been habituated to the presence of the hut and the apparatus from a previous study that made use of ropes instead of the handles of this experiment (Armster, 2018).

2.3 Individual Training

Phase I. The goal of the first phase of individual training was to help the monkeys form an association between the apparatus and food acquisition while giving them the opportunity to learn how to operate it individually. During this phase, the device was modified so that one of the pins holding the trapdoor in place was held permanently open. In this form, pulling on only one loop resulted in the trapdoor dropping open and simultaneous pulling provided no added benefit. This phase of individual training occurred between October 16, 2018 and November 10, 2018. The side actively required to operate the device was switched between the right and left side over the course of this phase to discourage perseveration of operation on only one side.

Each session of the individual training phase took place at least one hour after the scheduled morning feeding and begun with the manual release of the trapdoor of the apparatus, which makes a distinctive noise, to attract the attention of any monkeys in the area to the device. Each session consisted of a maximum of 10 successive trials. During each trial, the experimenter would lock food into the lockbox before moving off to the side or leaving the hut entirely so as not to obstruct access to the apparatus or affect the behavior of participating individuals. A trial was terminated if 15 minutes had elapsed since the apparatus was loaded and no potential pullers were currently displaying interest in the device. After trial termination, the trapdoor was again released to attract the attention of monkeys in the area, and the apparatus was reset. If a single individual operated the device for six successive trials within a session, the researcher left the experimental area for a short period of time (5-10 minutes) to prevent any one individual from monopolizing the device for an entire session and give other monkeys a chance to operate the device. A session was terminated if 1.5 hours had elapsed before 10 trials were completed, resulting in a minimum of six trials per session (in the event that six successive trials had been terminated at the 15-minute cutoff). A maximum of three sessions were run on any given day.

Two pieces of food were locked into the device during each trial to allow for study of reward division dynamics, thievery, and monopolization. The food items used in the training

sessions were apples, carrots, bananas, tomatoes, cucumbers, and potatoes, the relative reward value of which was determined in a previous study (Armster, 2018). The particular food combination used in a given session varied based on availability. Attempts were made to occasionally vary the reward items so as to maintain a high level of interest in the device, but the reward items most commonly consisted of apples (medium-quality) and bananas (high-quality). High-quality food items made up a portion of the available rewards in all sessions, but low-quality foods (such as carrots) were only incorporated into the mix when particular monkeys began monopolizing the apparatus and their presence needed to be dissuaded to give new monkeys an opportunity to gain experience with the device. Once the food items to be used for the day's sessions had been selected, their combination and usage order was randomized to prevent experimenter bias in reward selection. This randomization excluded low-quality food items, which were used as rewards only when a well-experienced monkey was monopolizing the device. On multiple occasions during the individual training phase, exclusively bananas were used during the session on an as-needed basis to provide additional motivation for newly interested individuals. On two occasions during phase one, food pellets were spread throughout the research hut and used as rewards in the apparatus to attract potential new device operators.

For an individual to qualify as having reached the criteria for being considered trained, they needed to successfully complete at least three trials split between two separate days. The first stage of individual training continued for 42 sessions. At the end of this phase, 11 monkeys had successfully met training criteria.

Phase II. The goal of the second phase of individual training was to help the monkeys learn that both loops needed to be pulled simultaneously in order to spring the trap door. During this phase, as in the first phase, the loops were positioned 20 centimeters apart so that it was possible for an individual to reach and pull both loops simultaneously. Unlike in the first phase, one of the pins was not permanently held open so that pulling both loops became necessary. The "simultaneous pull" training form of the device was used only with monkeys who had met training criteria in the previous phase. If potential new pullers began manipulating the loops, the apparatus was switched back to the "single-sided pull" form of the previous phase. This way, newly interested monkeys could still come to learn to use the device without having to begin with the more difficult "simultaneous pull" form, but more experienced pullers needed to learn the new contingency if they hoped to continue obtaining food. The one-sided version of the device was occasionally used with experienced monkeys as well on an as-needed basis to maintain a high level of motivation. Due to time constraints

in data collection, the second phase of training was to be concluded after a maximum of three weeks regardless of whether any monkeys had learnt the new contingency. This phase of training took place between November 11, 2018, and November 30, 2018, and continued for 36 sessions.

The session procedure used for this phase of training was identical to the procedure used in the first phase. By the end of this phase, 11 monkeys had reached training criteria on the "single-sided pull" form of the device but no monkey had met the training criteria on the "simultaneous pull" form.

2.4 Testing

During the testing phase of the experiment, the copper pipes from which the loop handles emerged were moved to a distance of 2 meters apart so that no single monkey could reach both loops simultaneously. In order to obtain the food in the lockbox, monkeys now needed to synchronize their operation of the two opposite loops. Testing took place from December 4th, 2018, to April 23rd, 2019, and consisted of 126 sessions.

Procedure. As in the training phases, sessions consisted of 10 trials and were conducted up to three times daily, the first of which was conducted at least one hour after the morning feeding. A trial was terminated if no monkey was successful in operating the device within 15 minutes unless there were monkeys actively interested in the device at that time in which case the trial continued until they succeeded or lost interest in the apparatus. If there was only one monkey actively interested in the device at the designated termination time, the experimenter attempted to act as a cooperative partner to give the individual an opportunity to gain experience with the device and ensure that the behavior of persistent individuals was occasionally reinforced. If a session continued for 1.5 hours without reaching 10 trials, the session was terminated. At the beginning of the session and any time that a trial was terminated due to lack of interest, the trap door was released to attract the attention of any monkeys in the area.

In each trial, two pieces of food were locked into the apparatus. Apples, bananas, tomatoes, and occasionally pineapples were the only food items used during the experimental phase so as to ensure that motivation levels remained high. The combination of food items and the order in which they were used with the apparatus was randomized during sessions. After loading the device, the experimenter moved to the edge of the research hut or left it entirely so as not to obstruct the monkey's access to the device or affect their behavior. If the food items were successfully retrieved from the apparatus, the experimenter returned to

repeat the setup procedure until the session had ended. If a single dyad was monopolizing the device, defined as succeeding in six successive trials, the researcher would leave the experimental area for a short period of time (5-10 minutes) to encourage those individuals to leave and provide a new dyad with an opportunity to use the apparatus.

Motivation Maintenance. During the first 10 sessions of the testing phase, the experimenter attempted to act as a cooperative partner for any persistently interested individuals even if the designated trial termination time had not been reached. This was done to give individuals an opportunity to learn the necessity of a cooperative partner in the early stages of the setup and decrease the likelihood that they would lose interest in the apparatus before acquiring an effective cooperative partner. An additional two motivational sessions of this sort were run later on during the testing phase to address a large decline of interest in the apparatus. These sessions were excluded from later analyses. On multiple occasions, exclusively bananas were used as rewards during a session to address other periods of low interest.

Multiple individuals who had met training criteria but failed to achieve early success with the cooperation phase completely lost interest in the device early on during the experiment. To address this issue, as well as to attract new pullers and introduce more variation into the pool of potential cooperative partners, the apparatus was switched back to the "single-sided pull" form and an additional training phase was carried out from January 29th, 2019, to March 10, 2019. During one session of this phase, peanuts were continuously spread throughout the hut to attract new individuals. This additional training phase ran for 51 sessions, and 13 individuals had met training criteria at its conclusion. After returning to the experimental setup, one further individual succeeded at meeting training criteria, bringing the total number of trained individuals up to 14. This additional training phase took place between Session 70 and Session 71 of the experimental phase.

2.5 Documentation

All sessions were fully recorded from two different corners of the research hut using cameras mounted in protective boxes in two opposite corners of the research hut. The cameras captured two different frontal angles of the experiment, ensuring that the entire apparatus was within view. During sessions and afterwards using the recordings, the trials were coded for identity of the pulling individual or individuals, identity of those unsuccessfully attempting to operate the device, identity of the individuals obtaining food, number and identity of the individuals in the surrounding area, what combination of food

items were used, and whether the pulling individual waited for a partner to arrive before pulling.

Defining an Attempt. An attempt was defined as "any manipulation of the loop using enough force to result in movement of the pin to the open position". The sound of the pin moving to the open position could be heard and the extent to which an individual had pulled the loop outwards could be readily determined from the session recordings. Relying on this strict definition of an attempt allowed for differentiation between deliberate pulling behavior and object exploration-based manipulations such as the play behaviors of infants. Multiple pulls occurring within a 5-second span were aggregated and counted as a single attempt. In coding an individual's attempts, separately coded columns served to distinguish whether there was a potential partner in the hut when the attempt was made and whether a potential partner was positioned in front of the opposite loop. A "potential partner" was defined as any individual who had previously succeeded in cooperation or met the training criteria. As a result, the presence of untrained individuals in the hut at the time of an attempt was not counted toward the partner presence classification.

Defining Waiting. An attempt was classified as a "wait" if it was preceded by the eventual puller delaying their pulling behavior for at least 15 seconds upon arriving to the area in front of the apparatus until such a time that a potential partner entered the area. Because waiting behaviors were defined as attempts preceded by a delay, cases where a partner did not arrive and trigger an eventual attempt were not counted as waiting behaviors even when lengthy delays were involved.

2.6 Analyses

To test whether individuals became increasingly proficient at cooperating over the course of the experiment, I ran a binomial generalized linear mixed model (GLMM) with a logit link function using "success" as the dependent variable and session number as a fixed effect. To control for repeated measurements, number of attempts and individual identity were added to the model as random factors. This analysis served to examine whether the proportion of successful attempts increased with the progression of the experiment, which would presumably reflect an increase in efficiency on the part of the pullers.

Separate binomial GLMMs with logit link functions were run on the variables "presence of partner within hut" and "presence of partner in front of loop" with session number as a fixed effect and number of attempts per individual as a random effect to control for repeated measurements. These analyses addressed whether individuals became more

sensitive to the presence of others over the course of the experiment and altered their behavior so as to pull more frequently in the presence of a potential partner. Testing the two variables separately allowed exploration of whether individuals were responding specifically to the presence of a potential partner in front of the loop or merely their presence within the area. These analyses were critically important in demonstrating that the monkeys were not pulling randomly and succeeding coincidentally. The implicit assumption here is that a change in the frequency of pulling in the presence of others is reflective of a change in puller sensitivity to the presence of others, presumably indicating an increasing recognition of the role that others play in their own success. An alternative explanation is that over the course of the experiment, the apparatus became more popular as its association with reward increased within the population. This may have led to an increase in the number of monkeys within the research area at all times, in which case an increase of pulling behavior in the presence of others over the course of the experiment would merely reflect an increased likelihood of others being present, rather than reflecting an increased sensitivity on the part of the puller. To correct for this possibility, the number of individuals present was added as a fixed effect to the model as well.

The presence of waiting behavior is another indicator that pullers are recognizing the role that others play in their own success and altering their own behavior accordingly. To assess if waiting behavior increased in frequency over the course of the experiment, I ran a binomial GLMM with a logit link function on the "waiting" variable with session number as a fixed effect and identity and number of attempts as random effects to control for the impact of repeated measurements.

To investigate whether cooperation amongst kin was more common than cooperation between non-kin, another binomial GLMM with a logit link function was performed on "success", this time with a variable representing whether or not a member of the puller's kin group was present in the hut as a fixed effect. Individual identity and number of pulls were again added to the model as random effects to control for repeated measures. Trials where no potential partners were present in the hut were excluded from the analysis.

A final analysis aimed to evaluate whether equitable division of the rewards was more or less likely amongst kin. To accomplish this, I ran a GLMM with a variable reflecting reward division (equal-division or one-takes-all) as the dependent variable and a second variable reflecting whether or not the dyad were kin as a fixed effect. Individual and dyad identity were added to the model as random effects to control for repeated measures. Unsuccessful trials and trials where thievery occurred were excluded from the analysis.

All statistical analyses were carried out using R statistical software (version 3.6.1; R Core Team, 2019) with α set at 0.05. GLMMs were run using the *lme4* package (Bates, Maechler, Bolker, & Walker, 2015). Pivot tables were created using the *dplyr* package (Wickham, François, Henry, & Müller, 2019) and plotted using the *ggplot2* package (Wickham, 2016).

Results

3.1 Descriptive Overview

Over the course of my experiment, I conducted 1165 trials spread across 126 sessions. Of these trials, 708 were successful, resulting in an overall success rate of 60.8% (708/1165). Twelve monkeys succeeded in cooperating in at least one instance. Individual results are summarized in Table 1. Four individuals who succeeded at least once in the training setup never engaged in cooperation and are excluded from this section. Of the cooperating individuals, only two were male. The age of participants ranged from 2 to 11, with an average of 6.1 (*SD*=2.8). Participants had an average of 118 successes (*SD*=183.7) and an average of 3.3 partners (*SD*=2.8). Overall, these individuals combined into 20 unique cooperative dyads, as summarized in Table 2. Three of those dyads were composed of kin, and those three dyads accounted 64.5% of all successful cooperations. Cooperative dyads had a mean of 35.4 successes (*SD*=67.2).

As detailed in Section 2.4, the first 10 sessions functioned as a transitionary period from the training to the experimental phase and were excluded from subsequent analyses. An additional 12 sessions were partially or completely excluded from subsequent analyses due to problems with the videos that made coding impossible. The cooperations that occurred during these sessions are still included in the summary tables. The excluded sessions were composed of a total of 202 trials, leaving 963 trials to be included in the analyses.

Table 1.
Summary of Results by Individual

Individual	Age*	Sex	Partners	First Success**	Total Successes
James	2	Male	11	Session 2	635
Ingrid	10	Female	3	Session 9	230
Pippi	2	Female	6	Session 3	203
Kate	7	Female	3	Session 36	177
Finn	5	Male	4	Session 5	78
Alina	11	Female	2	Session 6	58
Herta	6	Female	3	Session 5	14
Montana	8	Female	1	Session 107	10
Krato	5	Female	2	Session 73	5
Sandra	7	Female	3	Session 2	3
Julia	6	Female	1	Session 6	2
Kurtney	4	Female	1	Session 108	1

*: Age as of the beginning of the experiment. **: As detailed Section 2.4, a second training phase was run between session 70 and 71.

Table 2.
Summary of Results by Dyad

Dyad*	Partner Relationship	First Success**	Total Successes
James + Ingrid	Son-Mother	Session 9	228
James + Kate	Nephew-Aunt	Session 36	175
James + Pippi	Non-kin	Session 3	145
James + Finn	Non-kin	Session 6	64
Pippi + Alina	Daughter-Mother	Session 6	54
Finn + Herta	Non-kin	Session 5	10
James + Montana	Non-kin	Session 107	10
James + Alina	Non-kin	Session 90	4
Finn + Krato	Non-kin	Session 73	3
James + Herta	Non-kin	Session 80	3
James + Julia	Non-kin	Session 6	2
James + Krato	Non-kin	Session 81	2
James + Sandra	Non-kin	Session 2	1
Kate + Sandra	Non-kin	Session 83	1
Ingrid + Sandra	Non-kin	Session 84	1
Pippi + Herta	Non-kin	Session 95	1
Pippi + Kate	Non-kin	Session 97	1
Pippi + Finn	Non-kin	Session 103	1
James + Kurtney	Non-kin	Session 108	1
Pippi + Ingrid	Non-kin	Session 113	1

*: Only dyads with at least one successful cooperation are shown. All other possible dyadic combinations can be assumed to have zero successful attempts. **: As detailed in Section 2.4, a second training phase was run between session 70 and 71.

3.2 Proficiency

To examine whether cooperating individuals became more proficient at cooperating with experience, I ran a binomial generalized linear mixed model (GLMM) taking into account the relative frequency with which attempts resulted in success. As a fixed effect, I entered session number into the model. As a random effect, I had an intercept for number of pulls nested within individual to control for repeated measures. Over the course of the experiment, individuals did become more proficient at operating the apparatus (β=0.40, SE=0.04, z=10.30, p=<0.05) with the relative frequency of successful attempts increasing as a function of session (Figure 5). When breaking down the effect on the level of the individual, one can see that the effect of session on task success was not uniform across all subjects (Figure 6).
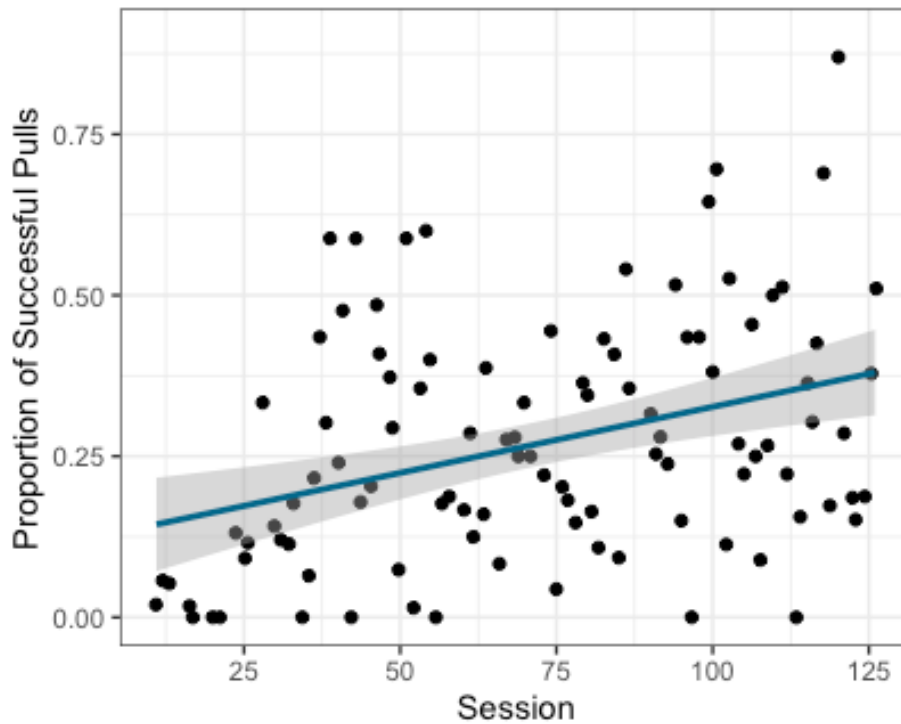
Figure 5. Scatterplot of proportion of successful pulls by session with line of best fit overlaid. Greyed area indicates standard error.
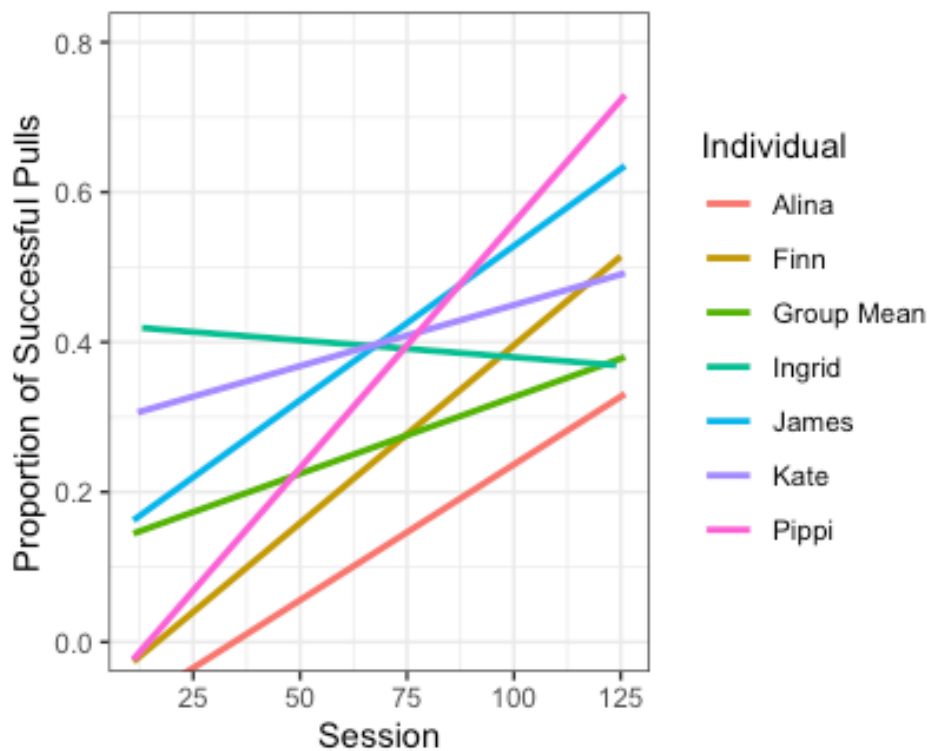

Figure 6. Line of best fit for proportion of successful pulls by session, broken down by individual with the group mean plotted for comparison. Only individuals with more than 50 successes are included.

To check the validity of the model, I performed an ANOVA comparing the full model with the effect under investigation to the model excluding that effect. The effect of success remained intact when compared to the null model ($\chi^2(1)$=107.07, p=<0.05).

3.3 Sensitivity to Partner Presence

To establish whether individuals came to recognize the role that others played as cooperative partners necessary for their own success, I examined the sensitivity of individuals to the presence of others over the course of the experiment. Making attempts in increasingly specific conditions (i.e., when a potential cooperative partner was present) was used as a proxy for understanding of the cooperative nature of the task and an indicator of deliberate rather than coincidental cooperation. The two indicators that I used to measure this were 1) the relative frequency of attempts being made in the presence of a partner, and 2) the presence of waiting behaviors in the absence of a potential partner.

To investigate whether attempts being made in the presence of a potential partner increased in relative frequency over the course of the experiment, I ran two separate binomial GLMMs. The first GLMM used the "presence of a potential partner within the hut" as the dependent variable while the second used the more rigorous specification of "presence of partner in front of loop". For both models, I entered session as a fixed effect as well as the number of monkeys present in the hut so as to control for the alternative explanation that attempts in the presence of partners only became more frequent because the research hut became more popular. As a random effect, I added number of attempts nested within individual identity to control for repeated measures. The presence-within-hut model failed to suggest any change in the rate of attempts in the presence of a potential partner (β=2.32, SE=1.98, z=1.18, p=0.24). The presence-at-loop model, on the other hand, revealed a significant decrease in the frequency of attempts being made in the absence of a potential partner over the course of the experiment (β=-0.16, SE=0.04, z=-3.67, p=<0.05; Figure 7). This effect remained intact even upon ANOVA-based comparison to a null model with only the number of monkeys present in the hut entered as a fixed effect ($\chi^2(1)$=13.54, p=<0.05). Examination of the effect on the level of the individual revealed considerable inter-individual variation in slope (Figure 8).

To examine whether the frequency of waiting behavior increased over the course of the experiment, I ran a binomial GLMM with a binary variable indicating whether or not waiting occurred prior to that attempt as the dependent variable. I added session to the model
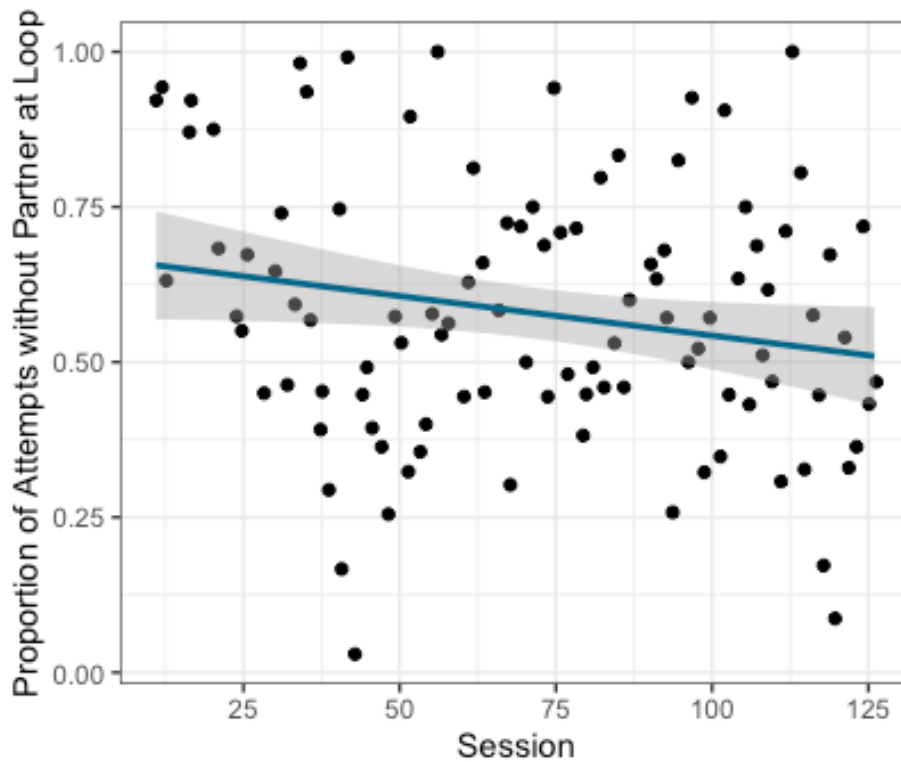
Figure 7. Scatterplot of overall proportion of attempts without a potential partner in front of the opposite loop. Line of best fit overlaid with surrounding greyed area indicating standard error.
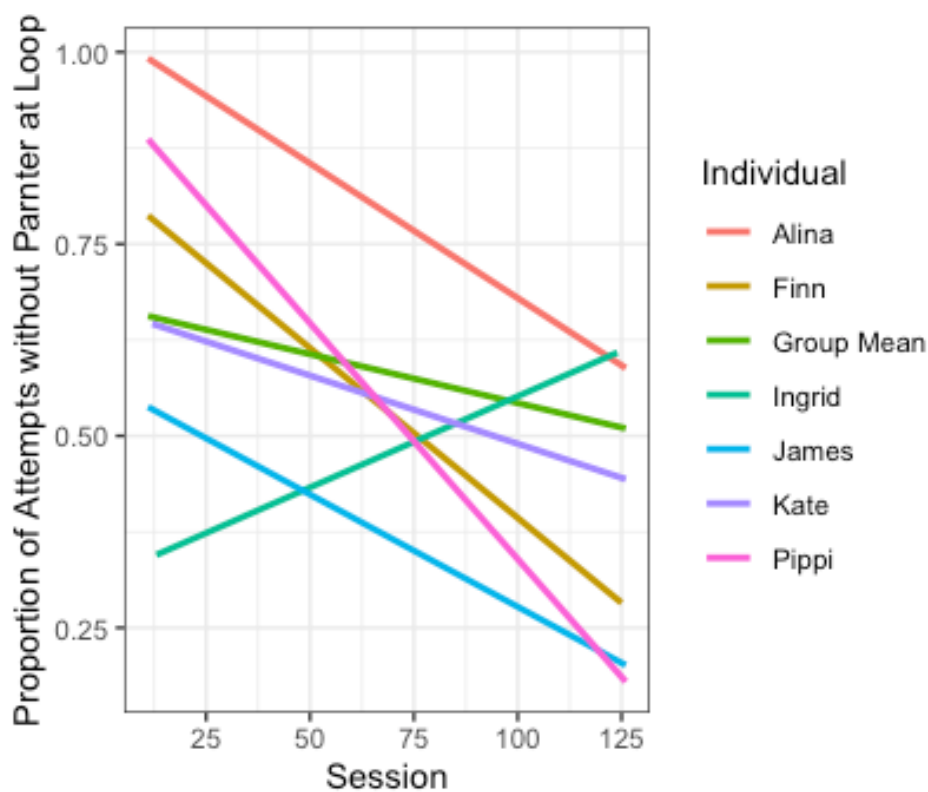
Figure 8. Line of best fit for proportion of attempts without a potential partner in front of the opposite loop, broken down by individual. Only individuals with at least 50 successes are included. Group mean has been added for comparison.

Figure 9. Bar graph showing instances of waiting per session with line of best fit overlaid. Greyed area indicates standard error.

Figure 10. Bar graph displaying total instances of waiting by individual. Individual labels are composed of the first two letters of the corresponding monkey's name.

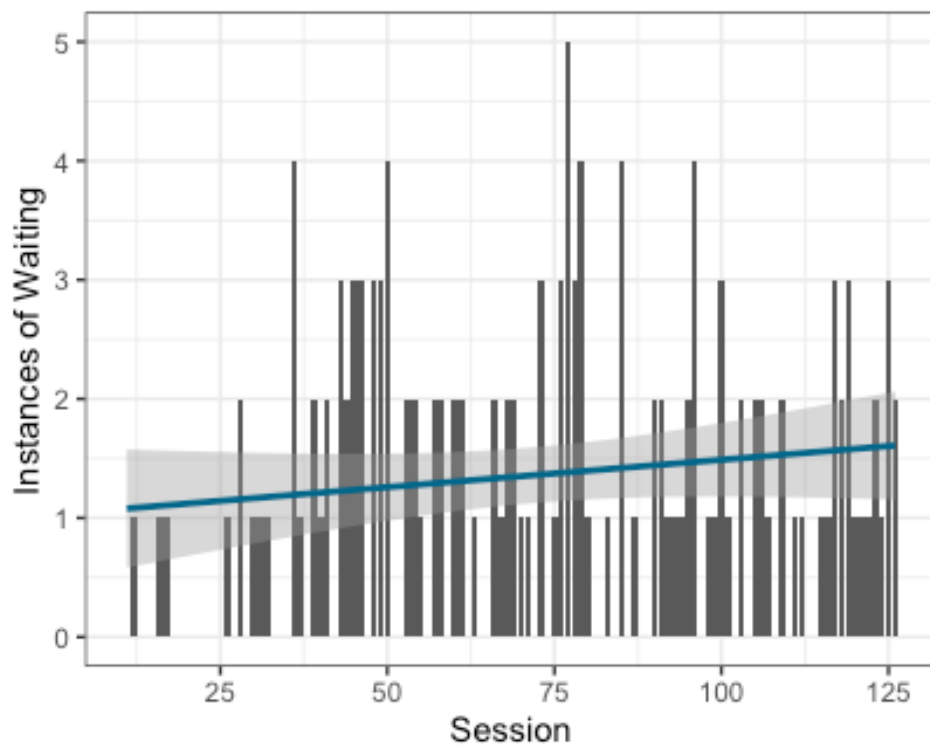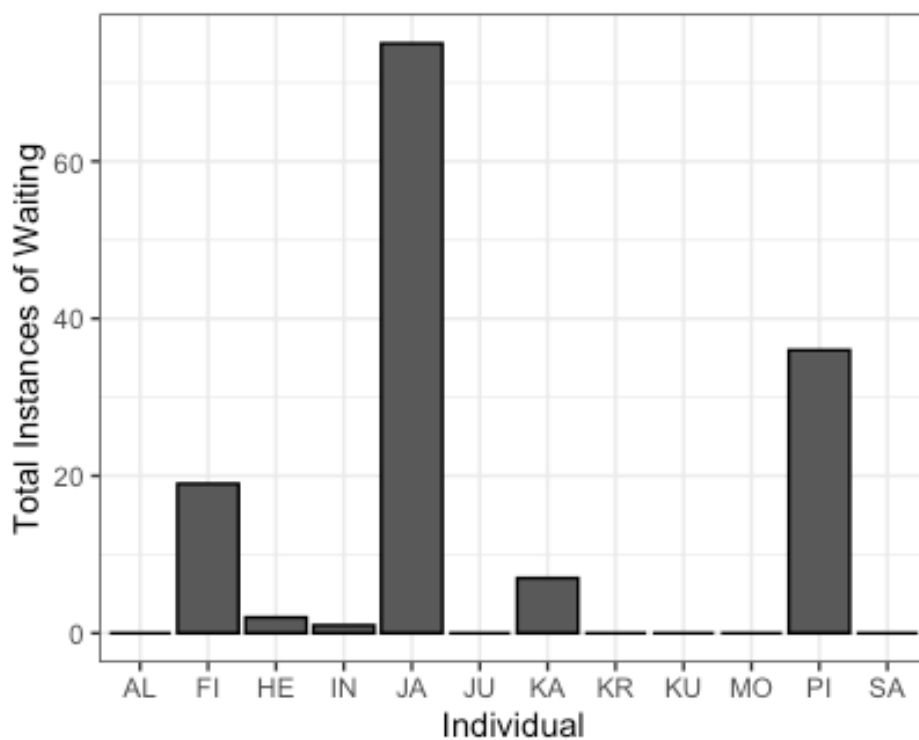as a fixed effect and number of attempts nested within individual identity as a random effect to control for repeated measures. The frequency of waiting behavior did increase over the course of the experiment as a function of session (β=0.38, *SE*=0.10, *z*=4.00, *p*=<0.05; Figure 9). The effect remained intact after ANOVA-based comparison to a null model (χ^2(1)=16.21, *p*=<0.05).

Examination of total instances of waiting on the individual level revealed that waiting was used as a strategy by only a few individuals (Figure 10), suggesting that the main effect of waiting results from the behavior of only a minority of the participating individuals.

3.4 Partner Preference

Twelve cooperating individuals paired off into 20 unique dyads, of a potential 66 unique dyads that could have occurred. The individuals belonging to family groups consisted of a mother-daughter pair and a mother-sister-son trio, which could have potentially formed four unique family dyads. Three out of four of those dyads (75%) did successfully form, and accounted for 64.5% of all cooperations. The three kin dyads that did form each included an individual below the age of three, suggesting a possible preference for cooperation with juveniles. Contrasting these results with the non-kin outcomes, there were 62 potential non-kin pairings of which only 17 manifested (27.4%). Of these 17 dyads, 13 included at least one individual below the age of three. On the whole, the non-kin pairings accounted for the remaining 35.5% of cooperations.

To test whether the apparent preference for kin partners was statistically significant, I performed a binomial GLMM on success with a binary variable representing whether or not kin were present within the hut as a fixed effect. Attempts made with no potential partners (neither kin nor non-kin) in the hut were excluded from the analysis. I added attempts nested within individual to the model as a random effect to control for repeated measures. The analysis failed to support the hypothesis that cooperation is more likely to manifest itself in kin than non-kin (β=0.06, *SE*=0.09, *z*=0.61, *p*=0.55).

3.5 Reward Division

Given that there were two rewards per trial and theft from individuals outside of the cooperating dyad was always a possibility, there were four ways that the rewards could be divided: an equal split between the cooperating dyad, one member of the dyad takes all of the rewards, one member of the dyad takes a reward and the other is stolen, or both rewards are

stolen. Of the 634 successful trials that were included in analyses, the food was split evenly in 312 instances (49.2%). One member of the dyad took all of the food 20.8% of the time (132/634 trials). Some form of thievery occurred in the remaining 30% of trials. In 174 of those instances, only one of the food rewards was stolen (27.4%) and in 16 instances both food rewards were stolen (2.5%).

To examine whether equal division of the rewards was more likely in kin or non-kin, I ran a binomial GLMM with a binary variable representing whether or not the reward division was equal as the dependent variable. Only successful attempts were included in the analysis and instances where thievery of one or both of the rewards occurred were excluded from the data set. A binary variable representing whether or not the cooperating individuals were kin was added to the model as a fixed effect. Individual identity was nested within dyad identity and included as a random effect to control for repeated measures. The analysis failed to suggest any major disparity in reward division norms between kin and non-kin dyads (β=-0.69, *SE*=0.96, *z*=-0.73, *p*=0.47).

Discussion

The primary aim of this thesis was to demonstrate that not only are Japanese macaques capable of cooperating to obtain food rewards, they understand the necessity of having a cooperative partner in the task. Demonstrating such an understanding is an essential step in arguing a case for deliberate cooperation on the part of the monkeys. Understanding of this aspect of the task needs to be assessed in terms of changing behavior over the course of the experiment. Specifically, I examined the proportion of attempts made in the presence of a potential partner as well as the presence of waiting behaviors. Statistical analysis demonstrated a behavioral shift in the predicted direction for both of these features, with a decrease in the proportion of attempts made without a potential partner and an increase in the frequency of waiting behavior. This led me to the conclusion that at least some of the individuals involved in my experiment developed an understanding of the contingencies of the task, including the necessity of having a partner, though they may not have understood the role that their partner played in the task.

My experiment further demonstrated that individuals became increasingly proficient with more experience, with successful attempts increasing in relative frequency to unsuccessful attempts as the experiment progressed. Though not a strong argument for task understanding in and of itself, when taken in conjunction with the increasing specificity in which participating monkeys made attempts, it bolsters the case for task understanding in at least some individuals. Increasing relative frequency of successful attempts is suggestive of greater coordination with cooperative partners.

Increasing specificity of pulling was evident in the case of most regular cooperators, but that doesn't necessarily mean that all of the monkeys who showed this pattern came to understand the cooperative nature of the task. For a dyad to give the appearance of deliberate cooperation, only one member of that dyad needs to be actively coordinating with the other. Increasing specificity of pulling as I measured it may just as easily indicate that another individual became adept at coordinating with them, rather than that they became good at coordinating with others. Used as a proxy for task understanding, increasing specificity of pulling needs to be interpreted with caution when taken in isolation. There was a significant main effect for an increase in the frequency of waiting behavior as well, but closer examination revealed that this behavioral strategy was only frequently used by three individuals. Given that all but two of the dyads that formed contained at least one of these individuals, it is a distinct possibility that all active coordination throughout the experiment rooted from them. Nevertheless, active coordination even in the case of only a few

individuals still demonstrates a capacity for task understanding and deliberate cooperation in the species, thus serving as proof of concept.

The three monkeys that frequently displayed waiting behaviors and were part of nearly all extant dyads were some of the youngest monkeys who took part in the experiment. A mental feature known as cognitive flexibility has been demonstrated to govern task-switching abilities and is known to decline with age in both humans and non-human primates (Manrique & Call, 2015). In a study of rhesus macaques, a species closely related to the subjects of my own experiment, Moore, Killiany, Herndon, Rosene, and Moss (2003) found that older monkeys had a greater tendency to perseverate on a previously learnt response pattern when a shift in behavioral strategy was required. The monkeys who took part in my experiment initially learnt how to operate the apparatus in a training form of the device that only required them to operate the device individually to obtain the food rewards. I suspect that when the apparatus was changed to its dyadic operation form, older monkeys had a more difficult time unlearning the reward contingency of the previous form, and this impaired their ability to learn the new reward contingency required of them. Behaviorally, this outcome would manifest itself in the form of perseveration on a previously successful strategy (i.e., treating the device as if it can be individually operated and ignoring the role of others). The higher level of cognitive flexibility present in the younger monkeys may have aided them in overwriting the old reward contingency more quickly, placing them in a position to come to understand the cooperative nature of the task.

To apply the results of my experiment to the levels of cognitive complexity discussed in detail in Section 1.1 (Boesch & Boesch, 1989), my participants demonstrably coordinated their actions both temporally and spatially, corresponding to their second highest level of understanding. Operationalizing this structure in the experiment-ready form of Chalmeau and Gallo (1996), at least some of my participants met the requirements for their second-level of understanding, in which an individual comes to operate the apparatus specifically when a partner is in position and success is possible. Theoretically, this level of understanding corresponds to a recognition on the part of the participant of the partner's role in the task. To demonstrate a higher level understanding, I would have needed to examine more closely whether participants engaged in information gathering with regards to their partner's actions. As this was not a focus of my thesis, one cannot rule out the possibility that the species possesses a greater level of understanding than I have demonstrated here.

An alternative explanation for the increase in the relative frequency of pulling behaviors in the presence of others is the possibility of social facilitation, a well-documented

phenomenon in which a dominant behavioral response is amplified in the presence of others (Zajonc, 1965). During the initial sessions of the experiment, individuals did not have as much experience with the apparatus so the dominant behavioral response may not yet have been pulling. As individuals gained more experience with the device and came to associate pulling with reward, pulling would have shifted to the dominant response and become amplified by the presence of others. This would result in the same pattern of behavior that I have argued is a result of increasing role awareness on the part of the cooperating individuals without invoking any special cognitive requirements. My argument against the social facilitation explanation is as follows: firstly, the effect of social facilitation should have been more or less constant across all individuals who came to associate pulling behavior with reward, but this was not the case. Some individuals that were highly-active in the experiment did not increase at all in relative frequency of pulling behaviors in the presence of others. One of the most successful individuals even showed a decrease by this metric over the course of the experiment, which is more in line with my assertion that only a few individuals gained insight into the cooperative nature of the apparatus and adjusted their behavior accordingly while others continued to make attempts more or less at random. Furthermore, extensive training sessions took place before the experimental phase began, so pulling behavior should have already been the dominant response at the beginning of the sessions used in the analyses and remained the dominant response throughout. Any effect of social facilitation should have therefore remained constant.

Another alternative explanation that needs to be countered in arguing that at least some of my individuals understood the role of others in the experiment is the possibility that they merely learnt the rule "pull when another individual is in front of the opposite loop". Learning this rule would result in a similar behavioral output of apparently coordinated pulling behavior, but would not require any insight on the part of the puller that their "partner" is actually taking part in the experiment as well. To argue against simple rule-learning as an explanation, one needs to look at the circumstances in which individuals did not pull. Infants were very frequently present in the research area and often engaged in exploratory play behavior with the loop. In the instances that I observed, these cases failed to evoke pulling behavior on the part of frequent participants, suggesting the possibility that they may discriminate between individuals capable of acting as cooperative partners and infants aimlessly manipulating the loop (infant monkeys were never observed to exert enough force on the loop during their play behaviors to trigger the trapdoor release). If they were merely following a "pull when another individual is in front of the opposite loop" rule, the

capabilities and behaviors of the opposite individual should not have resulted in a difference in the pulling behavior of experienced participants.

The fact that my experimental apparatus automatically reset itself after failed attempts was both a strength and a weakness of my study design. As a result of this design, making attempts in the absence of a partner was not specifically dissuaded. In the typical loose string paradigm, an attempt in the absence of a partner results in an inability to further participate in the experiment until the apparatus is reset by an attendant. With the apparatus used in my experiment, repeated attempts could be made without precluding the possibility of future attempts should a partner appear. In practical terms, this meant that the only cost of making an attempt on the device was the small energy input required of the attempt. This cost was likely low enough that the pressures acting toward the extinction of indiscriminate pulling were not strong enough to extinguish that behavior outright. On the positive side, this meant that individuals not met with immediate success at the apparatus could continue exploratory behavior with no ill effect until a potential partner appeared and gave them an opportunity to learn the appropriate reward contingency.

As for why indiscriminate pulling may have continued to occur even in the case of individuals who may have possessed an understanding of the task, the failure of pulling in the absence of a partner to extinguish completely may merely reflect a lack of behavioral inhibition abilities on the part of the participants. In a study of the closely related rhesus macaques *(M. mulatta)*, Evans and Beran (2007) concluded that the self-control capacities present in the species were inferior to that of humans and other great apes. The macaques in their study had a particularly difficult time maintaining self-control over a delay when an impulsive response option was continually available, as it was in my own study. Alternatively, pulling in the absence of a potential partner could represent an acquired strategy designed to attract the attention of others to the apparatus. The apparatus produced a distinctive sound with every attempt that was made on it, and this sound may have acted as a form of local stimulus enhancement, attracting the attention of others to the its source and increasing the likelihood that they would approach and manipulate it as well. Schwab, Swoboda, Kotrschal, and Bugnyar (2012) put forth a similar explanation to address the apparent lack of active signaling in their study of prosocial behavior in jackdaws. Though the jackdaws in their study did not directly recruit others or harass them into providing help, their own interactions with the apparatus served to attract the attention of others to it, thus increasing the likelihood that they would provide assistance. In my own study, manipulating the apparatus while others were within hearing range may have served a similar function,

which would help explain the failure of pulling in the absence of a partner to extinguish completely. Nevertheless, this explanation is highly speculative and requires further examination.

4.1 Social Factors

A key feature of this experiment is the fact that it was performed under naturalistic conditions, thus preserving the social environment of the monkeys and allowing for examination of social factors that may influence cooperation, such as partner selection and reward division. The descriptive statistics were highly suggestive of a preference for cooperation amongst kin, but further analyses failed to provide support for this hypothesis. It may be that kin relationships per se are not what determine cooperative dyad formation in the species, but the level of social tolerance between individuals. There were two non-kin dyads with upwards of 50 successful cooperations, both of which were composed of some of the youngest participants in the sample. Though Japanese macaques are generally a socially despotic species, the social constraints governing interaction norms may be more relaxed in the case of juveniles, as evidenced by their willingness to freely engage in play behaviors with one another (Norikoshi, 1974). Adult Japanese macaques, when they do engage in play behavior, have been demonstrated to do so much more readily with juveniles than with other adults (Ciani, Dall'Olio, Stanyon, & Palagi, 2012). In line with my own findings in Japanese macaques, Molesti and Majolo (2016) found in their study of cooperation in Barbary macaques that there was at least one juvenile cooperator in most successful dyads. Taking into consideration the apparent preference for both kin and juvenile partnerships, the best fitting explanation for the data may be that social tolerance mediates dyad formation, and the appearance of preference for kin and juvenile partners is an artefact of the higher level of social tolerance associated with those pairings. Social tolerance has been shown to be a major determinant of cooperation in other primate species such as chimpanzees (Melis, Hare, & Tomasello, 2006a) as well as corvid species such as ravens (Massen et al. 2015). In Japanese macaques specifically, Kaigaishi, Nakamichi, and Yamada (2019) concluded that inter-group variation in social tolerance is a large contributor to the expression of the species' cooperative capacities. That this pattern would be evident on the dyadic level as well is not surprising.

Another feature that sets my experiment apart from the majority of cooperation experiments is the deliverance of the rewards to a shared, monopolizable location rather than directly to the cooperating individuals. This allowed for examination of reward division dynamics within a social context more reminiscent of that which would be encountered by

the species under natural conditions. In nearly half of the successful trials, the rewards were split between the cooperating individuals. I hesitate to suggest that these even splits resulted from any sense of "fairness" possessed by the monkeys. The instances where a reward was left on the platform by one of the participants were few and far between, typically corresponding to trials where low-quality food was used as a reward, suggesting a rejection of the reward rather than an equity-directed decision. A simpler explanation of the high frequency of evenly split rewards is that, due to the cooperating individuals' equal distance from the reward platform, they were able to reach the rewards at roughly the same time and it was practically difficult for either of them to grab both rewards in this short span of time and escape successfully.

Thievery of one or both rewards occurred in 30% of all successful trials. In a previous study using an individual training form of the apparatus and the same pool of individuals, Armster (2018) found the rate of thievery to be 60.3%, far greater than that found in my own study. Given that the major methodological difference between my own study and that of Armster (2018) is the focus of mine on dyadic participation, it may be that a dyad can more readily monopolize the reward area than an individual. Armster (2018) also suggested that some of the monkeys were developing anti-theft strategies, and this may have decreased their susceptibility to reward theft. Another possible explanation to account for this discrepancy is then that participants fine-tuned theft-avoidance strategies over time that resulted in a lower rate of theft during the experimental phase of my own study.

4.2 Limitations and Criticisms

Defining waiting behavior was one of the larger conceptual obstacles in my thesis. Finding a way to operationalize waiting behavior is a paradox of sorts because the distinguishing feature of waiting is an absence of behavior. To take Hirata and Fuwa (2007) as a prototypical example of how others have handled the issue, they defined a wait within the context of the loose string paradigm as when "the subject took the rope, glanced at a partner who had not yet arrived at the rope, and did not pull the rope herself". This is a useful definition in that there is readily observable behavior (taking up the rope and glancing) paired with the non-behavior that is waiting. This is a fitting definition within the context of their more structured experiment, but with my more open-ended design during which any individuals can approach and operate the apparatus at any time of their choosing, the situation is more complicated. Individuals may arrive alone with a long delay before any potential partner enters the area. Even worse, a potential partner may never arrive even after that

prolonged period of waiting. I rejected using holding the loop in anticipation of a partner as a determinant of waiting because I felt given the hugely variable amount of time an individual may need to wait for a partner to arrive, it was unrealistic to expect them to hold the loop for the interim period. I likewise rejected using glancing behavior as a determinant of waiting because in most cases an individual waiting for a partner has no one around to glance at. Additionally, the target of any glancing that did occur could not always be determined because the open doorframes of the hut meant their glance could be directed to an area far outside of the camera viewpoint.

I settled on defining a "wait" as a period where the eventual puller arrived and remained in the area in front of the apparatus for at least 15 seconds without attempting to operate the apparatus, but began attempting to operate the apparatus when a potential partner entered the area. The observable feature defining the wait was then the initiation of pulling behavior in response to the arrival of a potential partner following a period absent of pulling behaviors. Whether that period of absent behavior persisted for only the minimum 15 seconds or continued for many minutes, the behavior was coded in the same way. This definition was not without its problems. For one, if a potential partner never appeared to trigger pulling, the waiting behavior was not coded at all, resulting in a potential underestimation of the frequency of waiting. The definition of waiting that I chose can thus be seen as a relatively conservative measure. Another issue with my definition is that it did not differentiate between different reasons that an individual may have been waiting for. If the eventual puller had been delaying acting due to the presence of a potential thief in the area, but the arrival of a partner caused the thief to leave and the waiting individual to begin pulling, this would also be classified as a wait despite the fact that the delaying individual may have only been waiting for the thief to leave. The occasional occurrence of these situations may have resulted in an overestimation of the frequency of waiting behavior. Taking these possibilities into account, the results pertaining to waiting in this thesis should be interpreted with caution.

A second issue with my experimental design was the fact that the viewpoint of the cameras recording the videos from which my behavioral coding was done did not cover the research hut in its entirety. The apparatus itself along with both pulling stations were always visible, so the "presence of partner at loop" variable should be accurate, but in some cases monkeys who were present in the hut may not have been visible in the videos. As a result, the "presence of partner in hut" variable probably underrepresents the frequency with which potential partners were in the hut while attempts were being made. This may have affected the outcome of the "attempts in presence of partner" analysis, potentially contributing to the

failure to detect any change in the "hut presence" form of that analysis. However, the key version of this analysis was the "loop presence" form, for which presence recordings are accurate, so the conclusion I reached remains unchanged regardless of the outcome of the "hut presence" analysis.

A factor that may have affected the "loop presence" analysis was my decision to only count individuals who had previously succeeded at operating the apparatus (during either the training or experimental phase) as potential partners. This decision meant that cases where experienced pullers appeared to be trying to coordinate their pulling with a never-before-successful monkey positioned at the other loop were counted as that individual making attempts in the absence of any potential partner. Regardless of whether or not these never-before-successful monkeys possessed any insight regarding operation of the apparatus, they may have been perceived as a potential partner and treated as such by experienced pullers. Defining "potential partner" in the way that I did resulted in a conservative measure that may have underrepresented participant sensitivity to the presence of others at the device. This underrepresentation renders the demonstrated pattern in the data all the more impressive because even with many attempts being in a sense misclassified as "partner absent" pulls, a significant effect was still present.

A potential issue with my behavioral coding was my decision to aggregate attempts into 5-second chunks, which resulted in dyads appearing more coordinated in my data set than they were in actuality. Though this aggregation heavily simplified behavioral coding of the videos, it was not always the case that an individual would only make one attempt within a 5-second span. For example, an individual might make 5 attempts in a 5-second span with only the final attempt lining up with their partner's attempt, but because these attempts were aggregated it would appear in my data set as if they had succeeded on their first attempt. The number of unsuccessful attempts should therefore be much higher than what is indicated in my data. This shouldn't have greatly affected the "attempts in presence of partner" analysis because the number of attempts would be similarly inflated in a both conditions. In the "proportion of successful pulls" analysis, the proportion itself would obviously be lower than reported, but I've no theoretical reason to suspect that the reported shift in proportion should not be retained assuming the deflation of attempt number was uniform across sessions.

4.3 Future Directions

Thierry (2000) arranges macaque species into a rough continuum of different forms of societal organization with some species being more on the despotic side while others are

more egalitarian. The different gradations of societal organization in otherwise roughly ecologically similar macaque species makes them a great testing grounds to study the impact of different forms of societal organization on the expression of social behaviors such as cooperation. Japanese macaques are ranked as one of the most despotic of the macaque species, but at present it is unclear whether this should promote or impede the expression of cooperative capacities. Molesti and Majolo (2016) conducted a cooperation experiment under similar conditions to my own with Barbary macaques, a species of macaques ranked by Thierry (2000) as much more tolerant than the Japanese macaques in my own experiment. At first glance, the monkeys in their study seemed to more freely form dyads with an average of 8.5 partners per individual compared to a 3.3 average in my own, but one needs to take into account their greater number of participants when interpreting this difference. Turning instead to the proportion of total possible dyads that formed, 93 out of a possible 325 dyads (28.6%) formed in their experiment compared to 20 out of a possible 66 dyads (30.3%) in my own. This cursory glance is not suggestive of any major difference in the cooperative capacities of the two species, though there were obvious differences between our studies in methodology and apparatus choice, so this comparison should not be taken too seriously. A second measure to take into account in comparing social tolerance between the two groups is the proportion of the total population that participated in the study. This feature is indicative of how readily members of the group are allowed near a food source and can be interpreted as a rough proxy for social tolerance within the group. In my own study, only 7.8% of non-infant monkeys (12/154) participated in at least one successful cooperation. Kaigaishi, Nakamichi, and Yamada (2019) report a similar participation rate in their own study of Japanese macaques, with only 5.8% of non-infant monkeys (18/312) taking part in their experiment. Contrast this with Molesti and Majolo (2016)'s study of Barbary macaques, in which 61.1% of non-infant monkeys (22/36) succeeded in at least one cooperation, and the difference is suggestive of a higher degree of social tolerance in the Barbary macaque group.

Study of this issue is further complicated by the within-species between-group differences suggested by Kaigaishi, Nakamichi, and Yamada (2019), who found large differences between the display of cooperative behavior between different groups of Japanese macaques. Considering the similarity in dyad formation rate between my study and that of Molesti and Majolo (2016), between-group differences may prove to be just as important as between-species differences with regards to cooperative behavior in macaques. A similar case can be made in genus *Pan*, where the reported difference in social tolerance between chimpanzees and the closely related bonobos (*Pan paniscus*; Cronin, De Groot, & Stevens,

2015) is difficult to interpret in light of the significant variance in social tolerance found between populations of chimpanzees (Cronin, van Leeuwen, Vreeman, & Haun, 2014). Whether a species-typical level of social tolerance can be determined for these species remains to be determined. Future study is needed before any clear conclusion can be drawn on the subject and finding the answer may not be as simple as running and comparing standardized between-species cooperation experiments.

Aggressive interactions occasionally occurred following cooperative interactions, but it was beyond the scope of my thesis to explore these interactions in depth. The occurrence of these aggressive interactions may have interacted with the quality of the rewards used or the reward division that occurred following cooperation. Aggressive interactions may serve to bully others into acting as partners in which case they may have a positive effect on cooperation, or they may simply represent squabbles over food rewards. The effect of aggressive interactions on subsequent cooperation is an interesting avenue of study deserving of future research. Another unresolved issue is whether reward division outcomes affect subsequent cooperations. It seems plausible that frequent unequal reward divisions will affect the likelihood that a monkey will choose to cooperate with that partner again in the future, as has been demonstrated in other species such as chimpanzees (Engelmann, Herrmann, & Tomasello, 2015) and ravens (Massen, Ritter, & Bugnyar, 2015). Without further study one cannot rule out the possibility that this particular species is insensitive to reward inequity.

Melis, Hare, and Tomasello (2006b) demonstrated that chimpanzees actively and selectively recruit partners when they are presented with a task that requires a partner, but it is an open question whether the monkeys in my study engaged in active recruitment attempts. One possibility is that individuals took advantage of the loud noise that the apparatus produced when an attempt was made to attract the attention of others who could potentially serve as cooperative partners. This would represent an active (albeit non-selective) attempt at recruitment and would help explain why pulling in the absence of a partner was never fully extinguished even in individuals who otherwise appeared to understand the nature of the task. I also observed repeated directed glancing from some of my participants that could have functioned as a signal to others to provide assistance. Alternatively, glancing may represent a heightened state of vigilance under circumstances where a dominant individual may appear at any moment, or information seeking with regard to the state of potential partners on the part of a puller. Chalmeau and Gallo (1996) used partner-directed glancing in their experiment as a key feature in demonstrating task understanding. Determining the target of glancing behavior in my experiment was practically difficult given the limited viewpoint of the

cameras, which impeded exploration of the subject in my experiment. Future research may wish to examine in more depth the conditions under which glancing behaviors occur and the function that they may serve.

Though all monkeys in the enclosure were given equal opportunity to approach the apparatus, a clear difference emerged between the sexes with very few males attempting to operate the device. The two males that did frequently take part in the experiment were considerably younger than the average age of the females in the experiment. The clear sex difference and near-complete absence of interest in adult males suggests the possibility that differing motivational drives or cognitive capacities, possibly triggered by the onset of puberty, influence approach and exploration behaviors in the species. Only two of the 18 Japanese macaques participating in Kaigaishi, Nakamichi, and Yamada (2019)'s cooperation experiment were male, and they had some of the lowest participation rates of their entire sample. My sample was not large enough to reach any firm conclusions on the subject, but it may be a worthwhile direction of study for future research.

Also warranting further investigation is the possibility that greater cognitive flexibility on the part of the younger monkeys may have aided them in learning the new reward contingency when the experiment shifted from the solo training version to its dyadic form. Systematic variance in participant cognitive flexibility has widespread implications not only for cooperation experiments, but for experimental design in the study of animal behavior on a more general level. The possibility that beginning my experiment with a solo training form may have led to perseveration of a previously learnt strategy that impaired learning of a new reward contingency calls into question the wisdom of designing experiments in this way.

4.4 Conclusion

My thesis set out to explore whether Japanese macaques are capable of succeeding in a cooperation-based task to obtain food. Special focus was given to determining whether individuals understood the nature of the task and the necessity of an experienced partner. The naturalistic conditions under which my experiment was conducted allowed for examination of partner choice and reward division in an intact social environment.

The evidence I have presented supports the existence of cooperative capacities in Japanese macaques. At least some, but almost certainly not all, of my participants had some understanding of the task and grew to better coordinate their actions with their partners over the course of the experiment. This was evidenced by an increasing ratio of successful attempts, an increasing likelihood to make attempts in the presence of a potential partner, and

an increasing likelihood to wait for a partner to arrive before making an attempt. Though most of the highly successful dyads in my experiment were made up of kin, analysis did not support a significant preference for kin in partner choice. Juveniles played a major role in the success of the experiment, with all of the highly successful dyads being composed of at least one juvenile monkey. Reward theft occurred in roughly a third of all cases, but the most frequent reward division was an even split between the cooperating individuals.

Despite the reputation of Japanese macaques as being some of the most socially despotic species of their genus, they have proven to be capable cooperators. The low level of social tolerance found in their species may impede widespread display of cooperative behavior by limiting potential dyadic interactions, but they can be quite adept at it within the pockets of interpersonal freedom allowed by their social organization.

References

Allem, S., Perry, C.J., Zhu, X., Loukola, O.J., Ingraham, T., Søvik, E., & Chittka, L. (2016). Associative mechanisms allow for social learning and cultural transmission of string pulling in an insect. *PLoS Biology, 14*(12):e1002589. doi:10.1371/journal.pbio.1002589

Armster, S. (2018). *The effect of different food rewards on performance in a string pulling task and subsequent theft avoidance in Japanese macaques (Macaca fuscata)* (Unpublished Master's Thesis). University of Vienna, Vienna.

Asakawa-Haas, K., Schiestl, M., Bugnyar, T., & Massen, J.J.M. (2016). Partner choice in raven (*Corvus corax*) cooperation. *PLoS ONE, 11*(6):e0156962. doi:10.1371/journal.pone.0156962

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1), 1-48. doi:10.18637/jss.v067.i01

Boesch, C. & Boesch H. (1989). Hunting behavior of wild chimpanzees in the Taï national park. *American Journal of Physical Anthropology, 78*(4), 547-573.

Boesch, C. (2007). What makes us human (*Homo sapiens*)? The challenge of cognitive cross-species comparison. *Journal of Comparative Psychology, 121*(3), 227-240. doi:10.1037/0735-7036.121.3.227

Bowles, S. & Gintis, H. (2003). Origins of human cooperation. In P. Hammerstein (Eds.), *Genetic and Cultural Evolution of Cooperation* (429-443). Cambridge, Massachusetts: MIT Press.

Burkhart, J.M., Allon, O., Amici, F., Fichtel, C., Finkenwirth, C, Heschl, A., ... van Shaik, C.P. (2014). The evolutionary origin of human hyper-cooperation. *Nature Communications, 5*(4747), 1-9. doi:10.1038/ncomms5747

Burton, J.J. (1977). Absence de comportement coopératif spontané dans une troupe de *Macaca fuscata* en présence de pierres appatées. *Primates, 18*, 359-366.

Call, J. & Tomasello, M. (1994). Production and comprehension of referential pointing by orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology, 108*(4), 307-317. doi:10.1037/0735-7036.108.4.307

Chalmeau, R. & Gallo, A. (1996). What chimpanzees (*Pan troglodytes*) learn in a cooperative task. *Primates, 37*(1), 39-47.

Chalmeau, R., Lardeaux, K., Brandibas, P., & Gallo, A. (1997). Cooperative problem solving by orangutans (*Pongo pygmaeus*). *International Journal of Primatology, 18*(1), 23-32.

Chalmeau, R., Visalberghi, E., & Gallo, A. (1997). Capuchin monkeys, *Cebus apella*, fail to understand a cooperative task. *Animal Behaviour, 54*(5), 1215-1225.

Ciani, F., Dall'Olio, S., Stanyon, R., & Palagi, E. (2012). Social tolerance and adult play in macaque societies: A comparison with different human cultures. *Animal Behaviour, 84*(6), 1313-1322. doi:10.1016/j.anbehav.2012.09.002

Crawford, M.P. (1937). *The coöperative solving of problems by young chimpanzees*. Baltimore: John Hopkins Press.

Cronin, K.A., Kurian, A.V., & Snowdon, C.T. (2005). Cooperative problem solving in a cooperatively breeding primate (*Saguinus oedipus*). *Animal Behaviour, 69*(1), 133-142. doi:10.1016/j.anbehav.2004.02.024

Cronin, K.A., van Leeuwen, E.J.C., Vreeman, V., & Haun, D.B.M (2014). Population-level variation in the social climates of four chimpanzee societies. *Evolution and Human Behavior, 35*(5), 389-396. doi:10.1016/j.evolhumbehav.2014.05.004

Cronin, K.A., De Groot, E., & Stevens, J.M.G. (2015). Bonobos show limited social tolerance in a group setting: A comparison with chimpanzees and a test of the relational model. *Folia Primatologica, 86*(3), 164-177. doi:10.1159/000373886

Cronin, K.A., Jacobson, S.L., Bonnie, K.E., & Hopper, L.M. (2017). Studying primate cognition in a social setting to improve validity and welfare: A literature review highlighting successful approaches. *PeerJ, 5*:e3649. doi:7717/peerj.3649

de Waal, F. & Luttrell, L.M. (1988). Mechanisms of social reciprocity in three primate species: Symmetrical relationship characteristics or cognition?. *Ethology and Sociobiology, 9*, 101-118.

de Waal, F. (2000). Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Animal Behaviour, 60*(2), 253-261. doi:10.1006/anbe.2000.1471

de Waal, F. & Berger, M.L. (2000). Payment for labour in monkeys. *Nature, 404*, 563.

de Waal, F. & Davis, J.M. (2003). Capuchin cognitive ecology: Cooperation based on projected returns. *Neuropsychologia, 41*(2), 221-228.

Drea, C.M. & Carter, A.N. (2009). Cooperative problem solving in a social carnivore. *Animal Behaviour, 78*(4), 967-977. doi:1016/j.anbehav.2009.06.030

Engelmann, J.M., Herrmann, E., & Tomasello, M. (2015). Chimpanzees trust conspecifics to engage in low-cost reciprocity. *Proceedings of the Royal Society B: Biological Sciences, 282*(1801): 20142803. doi:10.1098/rspb.2014.2803.

Evans, T. & Beran, M. (2007). Delay of gratification and delay maintenance by rhesus macaques (*Macaca mulatta*). *The Journal of General Psychology, 134*(2), 199-216. doi:10.3200/GENP.134.2.199-216

Halsey, L.G., Bezerra, B.M., & Souto, A.S. (2006). Can wild common marmosets (*Callithrix jacchus*) solve the parallel strings task?. *Animal Cognition, 9*, 229-233. doi:10.1007/s10071-006-0016-9

Hamilton, W.D. (1964). The genetical evolution of social behaviour I and II. *Journal of Theoretical Biology, 7*, 1-16 and 17-52.

Hauser, M.D., Chen, M.K., Chen, F., & Chuang, E. (2003). Give unto others: Genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back. *Proceedings of the Royal Society B: Biological Sciences, 270*, 2363-2370. doi:10.1098/rspb.2003.2509

Hirata, S. (2003). Cooperation in chimpanzees. *Hattatsu, 95*, 103-111.

Hirata, S. & Fuwa, K. (2007). Chimpanzees (*Pan troglodytes*) learn to act with other individuals in a cooperative task. *Primates, 48*(1), 13-21. doi:10.1007/s10329-006-0022-1

Jaakkola, K., Guarino, E., Donegan, K., & King, S.L. (2018). Bottlenose dolphins can understand their partner's role in a cooperative task. *Proceedings of the Royal Society B: Biological Sciences,* 285:20180948. doi:10.1098/rspb.2018.0948

Kaigaishi, Y., Nakamichi, M., & Yamada, K. (2019). High but not low tolerance populations of Japanese macaques solve a novel cooperative task. *Primates, 60*(5), 421-430. doi:10.1007/s10329-019-00742-z

Krams, I., Krama, T., Igaune, K., & Mänd, R. (2008). Experimental evidence of reciprocal altruism in the pied flycatcher. *Behavioral Ecology and Sociobiology, 62*, 599-605. doi:10.1007/s00265-007-0484-1

Manrique, H.M. & Call, J. (2015). Age-dependent cognitive inflexibility in great apes. *Animal Behaviour, 102*, 1-6. doi:10.1016/j.anbehav.2015.01.002

Marshall-Pescini, S., Schwarz, J.F.L., Kostelnik, I., Virányi, Z., & Range, F. (2017). Importance of a species' socioecology: Wolves outperform dogs in a conspecific cooperation task. *Proceedings of the National Academy of Sciences, 114*(44), 11793-11798. doi:10.1037/pnas.1709027114

Massen, J.J.M, Sterck, E.H.M, & de Vos, H. (2010). Close social associations in animals and humans: Functions and mechanisms of friendship. *Behaviour, 147*(11), 1379-1412. doi:10.1163/000579510X528224

Massen, J.J.M., Ritter, C., & Bugnyar, T. (2015). Tolerance and reward equity in ravens (*Corvus corax*). *Scientific Reports, 5*(15021). 1-11. doi:10.1038/srep15021

Massen, J.J.M., Behrens, F., Martin, J.S., Stocker, M., & Brosnan, S.F. (2019). A comparative approach to affect and cognition. *Neuroscience and Behavioral Biology Reviews, 107*, 370-387. doi:10.1016/j.neubiorev.2019.09.027

Melis, A.P., Hare, B., & Tomasello, M. (2006a). Engineering cooperation in chimpanzees: Tolerance constraints upon cooperation. *Animal Behaviour, 72*(2), 275-286. doi:10.1016/j.anbehav.2005.09.018

Melis, A.P., Hare, B., & Tomasello, M. (2006b). Chimpanzees recruit the best collaborators. *Science, 311*(5765), 1297-1300. doi:10.1126/science.1123007

Mendres, K.A. & de Waal, F. (2000). Capuchins do cooperate: The advantage of an intuitive task. *Animal Behaviour, 60*(4), 523-529. doi:10.1006/anbe.2000.1512

Molesti, S. & Majolo, B. (2016). Cooperation in wild Barbary macaques: Factors affecting free partner choice. *Animal Cognition, 19*(1), 133-146. doi:10.1007/s10071-015-0919-4

Moore, T.L., Killiany, R.J., Herndon, J.G., Rosene, D.L., & Moss, M.B. (2003). Impairment in abstraction and set shifting in aged Rhesus monkeys. *Neurobiology of Aging, 24*(1), 125-134. doi:10.1016/S0197-4580(02)00054-4

Noë, R. (2006). Cooperation experiments: Coordination through communication versus acting apart together. *Animal Behaviour, 71*, 1-18. doi:10.1016/j.anbehav.2005.03.037

Norikoshi, K. (1974). The development of peer-mate relationships in Japanese macaque infants. *Primates, 15*(1), 39-46.

Petit, O., Desportes, C., & Thierry, B. (1992). Differential probability of "coproduction" in two species of macaque (*Macaca tonkeana, M. mulatta*). *Ethology, 90*, 107-120.

Plotnik, J.M., Lair, R., Suphachoksahakun, W., & de Waal, F. (2011). Elephants know when they need a helping trunk in a cooperative task. *Proceedings of the National Academy of Sciences, 108*(12), 5116-5121. doi:10.1073/pnas.1101765108

R Core Team (2019). R: A language environment for statistical computing [Software]. R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org

Rose, L.M. (1997). Vertebrate predation and food-sharing in *Cebus* and *Pan*. *International Journal of Primatology, 18*(5), 727-765.

Scheid, C. & Noë, R. (2010). The performance of rooks in a cooperative task depends on their temperament. *Animal Cognition, 13*(3), 545-553. doi:10.1007/s10071-009-0305-1.

Schino, G. & Aureli, F. (2009). Reciprocal altruism in primates: Partner choice, cognition, and emotions. *Advances in the Study of Behavior, 39*, 45-69. doi:10.1016/S0065-3454(09)39002-6

Schwab, C., Swoboda, R., Kotrschal, K., & Bugnyar, T. (2012). Recipients affect prosocial and altruistic choices in jackdaws, *Corvus monedula. PLoS ONE, 7*(4):e34922. doi:10.1371/journal.pone.0034922

Schwing, R., Jocteur, E., Wein, A., Noë, R., & Massen, J.J.M. (2016). Kea cooperate better with sharing affiliates. *Animal Cognition, 19*(6), 1093-1102. doi:10.1007/s10071-016-1017-y

Stephens, D.W., McLinn, C.M., & Stevens, J.R. (2002). Discounting and reciprocity in an iterated prisoner's dilemma. *Science, 298*(5601), 2216-2218. doi:10.1126/science.1078498

Suchak, M., Eppley, T.M., Campbell, M.W., & de Waal, F. (2014). Ape duos and trios: Spontaneous cooperation with free partner choice in chimpanzees. *PeerJ*, 2:e417. doi:10.7717/peerj.417

Thierry, B. (2000). Covariation of conflict management patterns across macaque species. In F. Aureli & F. de Wall (Eds.), *Natural Conflict Resolution*, 106-128. Berkeley: University of California Press.

Trivers, R.L. (1971). The evolution of reciprocal altruism. *The Quarterly Review of Biology, 46*(1), 35-57.

Visalberghi, E. (1997). Success and understanding in cognitive tasks: A comparison between *Cebus apella* and *Pan troglodytes*. *International Journal of Primatology, 18*(5), 811-830.

Visalberghi, E., Quarantotti, B.P., & Tranchida, F. (2000). Solving a cooperation task without taking into account the partner's behavior: The case of capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology, 114*(3), 297-301. doi:10.1037/0735-7036.114.3.297

Werdenich, D. & Huber, L. (2002). Social factors determine cooperation in marmosets. *Animal Behaviour, 64*(5), 771-781. doi:10.1006/anbe.2002.2001

Wickham, H. (2016). ggplot2: Elegant graphics for data analysis. Springer-Verlag New York. URL: https://ggplot2.tidyverse.org

Wickham, H., François, R., Henry, L., & Müller, K. (2019). dplyr: A grammar of data manipulation. R package version 0.8.3. URL: https://CRAN.R-project.org/package=dplyr

Zajonc, R.B. (1965). Social facilitation. *Science, 149*(3681), 269-274.

Appendix A1: Abstract

Animal species vary in their cognitive ability to engage in various social behaviors, and those abilities may interact with the social environment of the species to form a complex behavioral profile. Cooperative capacities have been demonstrated in a wide range of species, but the specific factors relating to its emergence remain obscure. Until recently, research has focused on the cognitions involved in cooperation while neglecting the environmental features that promote and maintain it. I conducted a cooperation experiment in a population of Japanese macaques (*Macaca fuscata*) living under semi-naturalistic conditions. The experimental apparatus was housed in an open-air research hut that enabled any member of the population to approach and attempt to operate it at any point during the experiment. This setup ensured that the social environment of the macaques remained intact, enabling examination of partner selection dynamics in the species. The apparatus I used required individuals to simultaneously pull two loops in order to release two food rewards. The rewards were released onto a central platform in the research hut so as to allow for study of reward division following cooperation. Over the course of the experiment, individuals became more efficient at cooperating with one another which was reflected as a change in the ratio of successful to unsuccessful attempts. At least some individuals were sensitive to the presence of potential partners and learnt to wait for a partner to arrive before attempting to operate the apparatus. The most successful cooperative dyads consisted of family members or juveniles, suggesting social tolerance may have played a role in partner selection. Reward theft from individuals outside of the cooperative dyad occurred occasionally, but the rewards were most frequently split evenly between the dyad. In the discussion of my results, I give emphasis to addressing the extent to which individuals understood the cooperative nature of the task. Additionally, I discuss the social factors that may have contributed to dyad formation and stress the importance of maintaining an intact social environment to the highest degree possible in studies of social behaviors such as cooperation.

Appendix A2: Zusammenfassung

Tierarten variieren in ihren kognitiven Fähigkeiten, welche sie zu unterschiedlichen sozialen Verhaltensweisen befähigen. Diese kognitiven Fähigkeiten interagieren mitunter mit dem sozialen Umfeld der Tierart, was in einem komplexen Verhaltensprofil resultieren kann. Kooperative Kapazitäten konnten bereits anhand einer Vielzahl von Tierarten gezeigt werden, aber die spezifischen Faktoren, die dieses Verhalten bedingen, sind weiterhin unklar. Bis vor kurzem fokussierten sich Untersuchungen in diesem Forschungsfeld auf die in Kooperation involvierten Kognitionen, während umgebungs- und umweltbedingte Faktoren, welche Kooperation bedingen und aufrechterhalten, vernachlässigt wurden.

Für diese Arbeit wurde ein Kooperations-Experiment mit einem Bestand an in semi-natürlichen Lebensbedingungen gehaltenen japanischen Makaken (*Macaca fuscata*) wurde durchgeführt. Der experimentelle Apparat war in einer Freiluft-Baracke stationiert, was es jedem Mitglied des Bestandes ermöglichte, sich dem Apparat zu jeder Zeit während dem Experiment zu nähern und ihn zu betätigen. Dieser experimentelle Aufbau stellte sicher, dass das soziale Umfeld der Makaken intakt blieb, was eine Untersuchung der Dynamik der Partnerselektion ermöglichte. Der experimentelle Apparat musste von zwei Individuen mittels zwei Schlaufen gleichzeitig betätigt werden, um zwei Nahrungs-Belohnungen zu erhalten. Die Belohnungen wurden dann auf eine zentrale Plattform in der Baracke freigegeben, um Untersuchungen hinsichtlich der Belohnungs-Aufteilung nach der Kooperation zu ermöglichen. Im Verlauf des Experiments wurden Individuen effizienter in der Kooperation miteinander, was sich in einer Veränderung im Verhältnis der erfolgreichen zu nicht-erfolgreichen Betätigungen des Apparates zeigte. Zumindest einige Individuen waren sensibel hinsichtlich der Anwesenheit potentieller Partner und lernten auf diese zu warten, bevor sie versuchten den Apparat zu betätigen. Die erfolgreichsten kooperativen Dyaden bestanden aus Familienmitgliedern oder jüngeren Individuen, was einen Einfluss von sozialer Toleranz auf Partnerselektion naheliegend macht. Entwendung der Belohnungen durch Individuen außerhalb der kooperativen Dyade passierte von Zeit zu Zeit, aber meistens wurden die Belohnungen zu gleichen Teilen innerhalb der Dyade aufgeteilt. In der Diskussion der Resultate wird das Ausmaß, in welchem Individuen die kooperative Art der Aufgabe verstanden, ausführlich thematisiert. Des Weiteren werden die verschiedenen sozialen Faktoren diskutiert, welche zur Bildung von Dyaden beigetragen haben könnten, sowie die Wichtigkeit betont, im Rahmen von Forschung zu sozialem Verhalten wie etwa Kooperation ein intaktes soziales Umfeld aufrechtzuerhalten.