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Provisioning and Its Effects on the Social Interactions of Tibetan Macaques (*Macaca Thibetana*) at Mt. Huangshan, China

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PROVISIONING AND ITS EFFECTS ON THE SOCIAL INTERACTIONS OF

TIBETAN MACAQUES (*MACACA THIBETANA*)

AT MT. HUANGSHAN, CHINA

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by

Brianna Schnepel

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Graduate Studies

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ABSTRACT

PROVISIONING AND ITS EFFECTS ON THE SOCIAL INTERACTIONS OF

TIBETAN MACAQUES (*MACACA THIBETANA*)

AT MT. HUANGSHAN, CHINA

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Brianna Schnepel

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The dispersal patterns of food resources has a significant effect on the composition of primate groups and social interactions within those groups. Humans often alter the dispersal of food. Non-humans often use affiliative behaviors to elicit tolerance or support from other group members. I investigated whether provisioned food resources alter the social interactions and group dynamics of *Macaca thibetana*. All-occurrence sampling and scan sampling were used for data recorded by camera traps. Trail-cameras were placed at six locations that contain natural and human food resources and recorded 60-second videos. Social behavior and proximity of the monkeys were recorded. I found that *M. thibetana* maintain closer proximity while in non-provisioning areas at Mt. Huangshan. The data also shows that they exhibit higher levels of agonistic and submissive behavior while in the provisioning areas than while in the non-provisioning areas, and they engage in more affiliative behaviors while in non-provisioning areas than while in provisioning areas.

Keywords: primate behavior, foraging strategies, animal behavior, Tibetan macaques, *Macaca thibetana*, ecology

ACKNOWLEDGEMENT

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CHAPTER I

INTRODUCTION

Primates, including humans, often live in social groups which may vary with regards to demographics and structure. The foraging strategies adopted by female primates may determine group composition, because male primates act in ways that provide them better access to mates (Wrangham, 1980). Four different types of intra- and inter-group feeding competition have been applied to group living animals: within-group competition (WGC), within-group scramble (WGS), between-group competition (BGC), and between-group scramble (BGS). WGC or BGC usually occur when a food resource is dispersed in a clumped, more defensible pattern and results in strong dominance hierarchies. WGS or BGS is common when food is more evenly distributed and is difficult for one individual or group to monopolize, which leads to weaker dominance hierarchies (Isbell & Young, 2002; Janson & van Schaik, 1988; Koenig, 2002; van Schaik, 1989; Sterk, Watts, & van Schaik, 1997). Primates living in hierarchical groups use a variety of strategies to gain access to resources (e.g., food and mates). One strategy that is often used by social living primates is to use affiliative behaviors, such as grooming, as a way to form and maintain social bonds in order to receive more tolerance from other group members and lower the aggression directed towards them (Barrett, Heinzi, Weingrillm Lycett, & Hill, 1999; Carter, Macdonald, Thomson, Goldizen, 2009; Seyfarth, 1977; Silk et al., 2010; Tiddi, Aureli, Sorrentino, Janson, & Schino, 2011).

Non-human primates sometimes find human food resources and utilize them as an alternative food resource when living in anthropogenic environments, which may lead to tension between the species (Albert, Huynen, Savini, & Hambuckers, 2013; Fuentes & Gamerl, 2005; Radhakrishna, Huffman, & Sinha, 2013; Riley, 2007; Sha, Gumert, Lee, Jones-Engel, Chan,

Fuentes, 2009; Knight, 2011). This tension is sometimes thwarted by humans providing food for the non-human primates and capitalizing on them as a tourist attraction (Knight, 2011). Tourism sites vary with respect to ecosystem, financial systems, political systems, with many different aspects of relevance to the evolution of the primates. There has been little systematic research on the sustainability of tourism sites (Fuentes, 2006; Fuentes, 2004; Hsu, Kao, & Agoramoorthy, 2009; Knight, 2011; Orams, 2002).

Altered habitats and new food sources affect primates' social structure and group composition. Humans often distribute food in a clumped, uneven manner when provisioning other primates (Asquith, 1989; Berman & Li, 2001; Fa, 1986; Fuentes & Gamerl, 2005; Furuichi, 1983; Hill & Okayasu, 1995; José-Domínguez, Huynen, García, Albert-Daviaud, Savini, & Asensio, 2015; Orams, 2002; Unwin & Smith, 2010). Furuichi (1983) found that macaques provisioned with human food who were able to remain further away from other group members had lower levels of aggression than did groups whose members remained in closer proximity. Human food resources have been shown to be easier to digest and more nutrient rich than natural food resources, which makes them more appealing to nonhuman primates. Consequently, more intense levels of aggression are often exhibited by primates while foraging on human-provided food (Asquith, 1989; Mori, 1977; Fa, 1986; José-Domínguez et al, 2015; Orams, 2002 Riley, Tolbert, & Farida, 2013).

Primate research requires access to a primate groups that are habituated to human presence so that the primates do not alter their behavior when humans are near (Doran-Sheehy, Derby, Greer, & Mongo, 2007; Williamson & Feistner, 2003). The process of habituating primates is long and arduous. To speed the habituation process, researchers sometimes provision with food, which may alter primates' behavior of by increasing competition which increases

aggression. The technology in the form of camera traps provides an alternative to habituation. Camera traps are triggered by movement and take still photographs or video (Bezerra et al., 2014; Gerber, Williams, & Bailey, 2014). These can be used to collect detailed behavioral records without habituation and the provisioning that sometimes accompanies it. Few studies have explored the impact of provisioning on primates' behavior through comparison of behavior near provisioning sites and away from it.

The present study focuses on the foraging behavior of provisioned *Macaca thibetana*, with camera traps used to collect behavioral data when the monkeys are in compared to away provisioning sites. *M. thibetana* are found in central-eastern China. Females are philopatric. Their groups have a linear dominance hierarchy. Maternal kin relations have been shown to affect the social interactions within the group. *M. thibetana* are more tolerant of closely related kin and engage in more affiliative behavior toward kin compared to other individuals (Berman, Ogawa, Ionica, Yin, & Li, 2008).

Nearly all published research on *M. thibetana* comes from provisioned troops and little to no research has been conducted on their natural diet or behaviors while foraging on natural food (Berman, Ionica, & Li, 2004; Fooden, 1982; Zhang, Wang, & Quan, 1981). I studied the potential effects that provisioning has on social behaviors and group dynamics of *M. thibetana* living in Mt. Huangshan, China. I tested two hypotheses: 1. *M. thibetana* will exhibit different levels of agonistic, submissive, and affiliative behaviors in provisioning and non-provisioning zones. I predicted that levels of agonistic and submissive behaviors would be higher in the provisioning zones and levels of affiliative behaviors would be higher in non-provisioning zones. 2. Subjects will maintain different inter-individual distances in the provisioning and non-provisioning areas. I predicted that subjects would maintain closer proximity in the provisioning

zones because of how provisioned food was distributed. I also tested the efficacy of using camera

traps to collect behavioral data at this site.

CHAPTER II

LITERATURE REVIEW

Camera Studies

Primate researchers face many obstacles while collecting data on non-human primate species, and central among these is the elusiveness of primates. Primate species may evade researchers, hindering the data collection process. Primate researchers habituate non-human primate study groups prior to most data collection. This process takes considerable time and effort, including years of tracking groups of primates, persistently following subjects at a distance, and knowledge of the species' behavioral repertoire (e.g., activity patterns, foraging strategies, dominance structure, etc.) (Ando, Iwata, & Yamagiwa 2008; Bezerra et al., 2014; Doran-Sheehy et al. 2007; Thompson, 2004; Williamson & Feistner, 2003). Advances in technology, such as camera traps, are beneficial to primate studies (Bezerra et al., 2014; Farris, Karpanty, Ratelolahy, & Kelly, 2014; Galvis, Link, & Di Fiore, 2014, Gerber, Williams, & Bailey, 2014; Pebsworth & Lafleur, 2014). Camera traps have become more widely used by primatologists and may play a crucial role in future conservation and management practices of many primate species (Bezerra et al., 2014; Farris et al., 2014; Loken, Spehar, & Rayadin, 2013; Pebsworth & Lafleur, 2014).

Pebsworth and LaFleur (2014) outline possible methods for camera studies and stress the importance of selecting the correct camera with appropriate functions such as flash, trigger speed, sensitivity, range of detection, and security. Camera placement is important, and depending on the research question, must be random (Gerber et al., 2014) or strategic (Loken et al., 2013; Pebsworth & Lafleur, 2014). The number of cameras is determined by the research question and funds (Pebsworth & Lafleur, 2014). When funds for cameras are limited it appears

that spreading the cameras around and creating more camera trap locations is more beneficial than placing more cameras at fewer trap locations (Farris et al., 2014; Gerber et al., 2014; Pebsworth & Lafleur, 2014). When multiple cameras are placed at a single camera trap location, it is important to outline the criteria for independent captures in order to avoid pseudo replication (Bezerra et al., 2014; Farris et al., 2014).

Camera traps have also been used to record a population's behavioral flexibility. In order to better understand the relationships between predators and primates Farris and colleagues conducted an investigation of the co-occurrence of predators and primates in Northeastern Madagascar. They sampled the activities and distribution of Lemuridae and those of endemic and introduced predators in different forest types using photographic line transects (Farris et al., 2014). A camera trapping grid containing 23-25 camera stations that were placed roughly 500m apart was constructed for each study site. The camera traps provided evidence for a decline in the abundance of both endemic predators and lemurs in fragmented forests and an increase of introduced predators in this forest type. However, both lemurs and endemic predators outnumbered introduced predators in contiguous forests that are dwindling and are critical for many species of lemurs and predators alike (Farris et al., 2014).

Researchers have used camera traps to study specific behaviors of non-humans. Head and colleagues used video-camera traps in Loango National Park, Gabon to quantify the habitat use and competition for resources among *Pan troglodytes troglodytes* (African chimpanzee), *Gorilla gorilla gorilla* (western gorilla), and *Loxodonta cyclotis* (forest elephant). The video-cameras were distributed evenly throughout four forest types and were set to record 60 seconds of video immediately when triggered. The videos demonstrated which resources were important to the three species and the differences between the ways in which elephants competitively exclude

both chimpanzees and gorillas when there are limited resources. The researchers were able to determine that chimpanzees compete with elephants more for fruit, while gorillas compete more with elephants for herbs by observing the behaviors of all three species that were captured in the video data (Head, Robbins, Mundry, Makaga, & Boesch, 2012). Until recently, only anecdotal observations have existed on the degree of terrestriality of *Pongo pygmaeus* (Bornean orangutan). Loken and colleagues (2013) systematically set out camera traps in Wehea Forest to gain information on the contexts under which different age-sex classes of orangutans may come to the ground. The authors found that orangutans were photographed on the ground almost as frequently as pig-tailed macaques (*Macaca leonine)* (Loken, Spehar, & Rayadin, 2013). The terrestrial behavior of orangutans in the different contexts by both sexes may not have been observed without the camera traps as human presence can still alter the behaviors of even the most habituated non-human primates.

All of the previous research with camera traps has shown that trail cameras are an effective technique for gathering behavioral data. The current study relied on the effectiveness of camera traps to gather data on social behaviors in different contexts (around human food resources and around naturally occurring food resources). Each trap location contained only one camera. This allowed for more camera trap locations, which the literature has demonstrated to be beneficial (Farris et al., 2014; Gerber et al., 2014; Pebsworth & Lafleur, 2014). Camera traps were strategically placed, rather than randomly placed, in order to obtain ample data. They were also moved several times in order to find the best locations (Loken, Spehar, & Rayadin, 2013).

<div style="text-align:center">Studies of Foraging Strategies</div>

Foraging strategies are integral to explanations of primate group compositions and social behaviors. Many researchers have offered theories on the effects that food distribution has on

group structure and social interaction of social primates. One such researcher is Richard

Wrangham (1980), who focused on female-bonded social groups. In female-bonded groups

females' social interactions (e.g., affiliation, aggression) have a significant effect on the group's

dominance hierarchy and cohesiveness. In Wrangham's model, female behavior is determined by

ecological variables such as resource availability. Males adapt their behaviors in ways that allow

them sexual access to females. When females work together to defend their resources, a female-

bonded group is formed. Males may play an essential role in resource defense in these groups,

which, in turn, gives them access to and possible control over food resources and females with

whom to mate (van Schaik, 1989; Wrangham, 1980).

Terborgh and Janson (1986), among others (e.g., Isbell & Young, 2002; Janson & van

Schaik, 1988; Richter, Gras, Hodges, Ostner, Schulke, 2015; Sterk et al., 1997; Teichroeb &

Janson, 1986; Wheeler, Scarry, Koenig, 2013, van Schaik, 1989), suggested that previous

theories of primate social organization might have de-emphasized ecological factors, such as

predation and infanticide, that affect primate group size. Primate researchers suggested that all

ecological aspects must be accounted for when attempting to understand the evolution of primate

groups. Van Schaik (1989) proposed an extension to Wrangham's theory by postulating that

female primates compete for resources with other females who are both within and outside of

their social group. He also claimed that predation risks affect group size, cohesion, and within-

group competition. He hypothesized that predation influences female cohesiveness within a

group: females that experience higher levels of predation risk should form more cohesive groups

than those that experience lower levels of predation risk.

Van Schaik (1989) outlined four different types of intra-group and inter-group

competition in non-human primates. WGS occurs when food is distributed in either small or

large patches that cannot be controlled by a small subset of the group; thus, all individuals share the limited supply. No individual benefits more than any other in this type of competition, and this competition often affects group size. WGC occurs when a subset of a social group controls a food resource and gains a higher net food intake than the average group-mate. This type of competition typically results in a more defined dominance hierarchy within the group. Dominant individuals forage on higher quality food items and deter subordinate individuals from doing so, thus forcing them to forage on lower quality food items. This benefits the fitness of the dominant individual at the cost of the subordinate individual's fitness. BGC occurs when there are higher rates of aggression between groups with overlapping home ranges, or food is dispersed in a way that allows one group to defend it. In this type of competition, a larger or more dominant group can monopolize a food resource. The dominant group restricts the access of the less dominant group to the food resource. The fitness of members of the subordinate group is compromised, while fitness of the members of the dominant group is enhanced in this type of competition. BGS occurs when it is impossible for one group to control food resources. Groups involved in BGS usually live in overlapping home ranges, and the fitness of all individuals is equally affected by the available resources (van Schaik, 1989)

Social Interactions

Group composition is also affected by individual social relationships, which are expressed through agonistic, submissive, and affiliative interactions. Primate groups with a high level of WGC exhibit high levels of agonistic displays and aggression. Dominant individuals often monopolize defensible food resources of high value, and subordinate individuals avoid or abandon food resources when higher-ranked group members are present (Barton, Byrne, Whitten, 1996; Koenig, 2002; van Schaik, 1989; van Schaik & van Noordwijk, 1988; Teichroeb,

White, Chapman, 2015; Vahl, Lok, van der Meer, Piersma, Weissing, 2005; Vogel & Janson, 2007). Shopland (1987) found that *Papio cynocephalus* (yellow baboons) are more likely to interrupt another individual's foraging bout when the individual is feeding on a food items that are easier to process, and interrupted individuals are more apt to abandon the food resource while foraging on a food resource that requires a lower investment of time and energy. This observation led the author to postulate that, when attempting to displace an individual, interrupters determine their chances of success based on the food resource of the interuptee. Shopland (1987) also suggested that the interrupter might interrupt individuals in an effort to exhibit dominance. In species with linear dominance hierarchies, such as *Chlorocebus pygerythrus* (vervet monkeys), higher-ranked individuals control patchy food resources and prevent lower-ranked individuals from gaining access to these food items, thus increasing the fitness of the dominant individuals at the expense of the subordinate individuals (Whitten, 1983). Through agonistic displays, dominant vervets maintain priority of access to certain food resources by monopolizing patchy food. Vervet monkeys have a breeding and birthing season, and priority of access is also correlated with higher birth rates. Females that maintain more access to food reproduce earlier in the season, wean their infants earlier, and are subsequently able to reproduce earlier in the following season. However, the survival rate is not increased for offspring of more dominant individuals (Whitten, 1983).

Primates that live in groups with a hierarchical social structure may use many strategies to maximize their nutrient intake and minimize the amount of agonistic interactions directed towards them. Seyfarth (1977) outlined a model for social grooming in adult female monkeys. He reasoned that being groomed is beneficial to animals because ectoparasites are removed. He also argued that grooming others is beneficial to animals because it helps the groomer gain

support from the groomee. He suggested that it would be more beneficial to groom higher-ranking individuals, which may create competition for grooming partners. However, the amount of time spent grooming more preferred group members could be constrained by other needs (e.g., infant care, foraging).

Grooming may also be exchanged for tolerance during foraging from other group members (Barrett et al., 1999; Stammbach & Kummer, 1982; Tiddi et al., 2011). Tiddi, Aureli, Sorrentino, Janson, and Schino (2011) observed the differences in tolerance of tufted capuchins (*Cebus paella nigritus*). The study aimed to determine if more tolerance was given to subjects who had groomed dominant individuals within two hours prior to feeding, if more tolerance was given to subordinates who groomed dominants more frequently, or both. The data indicated that tufted capuchin monkeys use an effective strategy of grooming other group members to receive tolerance in return, but time since last grooming did not appear to be an important factor. Higher rates of grooming occurrences by subordinate individuals did elicit more tolerance from dominant individuals directed toward subordinates. The authors suggested that grooming may be used as a currency among primate groups that may be traded for tolerance during more than just foraging (e.g., mating) (Tiddi et al., 2011).

Feeding rate and the size of a feeding group an individual is observed in may be significantly varied even when looking at a single subject. In an effort to avoid agonistic interactions, subordinate animals may completely avoid a food patch. Alternatively, subordinate animals may alter their feeding rate depending on the food patch and the presence of more dominant individuals (Kazahari, Tsuji, & Agetsuma, 2013). Lower-ranking individuals may become more submissive while feeding in a smaller patch of food with higher rates of contest competition. Another strategy that animals use to avoid aggression while foraging is foraging

with individuals of a similar rank. This allows individuals to allocate more time to foraging rather than responding to agonistic threats from more dominant group members (Barton et al., 1996; Saito, 1996; Kazahari et al., 2013; Koganezawa & Imaki, 1999). Animals may also choose to forage with individuals who they have formed affiliative bonds with through frequent grooming and other affiliative behaviors (Barrett et al., 1999; Stammbach & Kummer, 1982; Tiddi et al., 2011). Subordinate individuals often compensate for their lower rate of nutrient intake by beginning to feed earlier or ceasing to feed later in the day (Saito, 1996). Janson (1985) found that in brown capuchins (*Cebus apella*) subordinate individuals consume less than dominant individuals. Levels of aggression had a significant effect on the amount of food consumed. When high levels of aggression were exhibited at food resources, high-ranking individuals consumed more than low-ranking individuals, and when no aggression occurred at food sources, all group members consumed equal amounts of food. The level of within-group competition was ten times greater than the level of between-group competition (Janson, 1985).

Food Distribution

A tolerance/intolerance (T/I) distance may exist within primate groups, which influences the intra-group levels of agonistic displays and aggressive interactions. This distance may be shorter than the average distance between individuals that are in a feeding group. The T/I distance may have a greater effect on WGC than the dominant-subordinate relationship in some primate groups (Furuichi, 1983; Hanya, 2009; Mori, 1977; Shopland, 1987; Vahl et al., 2005). Furuichi (1983) observed a troop of *Macaca fuscata* (Japanese macaque) and concluded that agonistic interactions were more common when macaques were in closer proximity than when individuals within the group maintained a greater distance. Furuichi (1983) also noted that agonistic interactions often ended when individuals returned to the accepted T/I distance. All

group members avoided approaching other group members who were foraging, regardless of rank. Lower-ranked individuals were able to move about as freely as higher-ranked individuals when the T/I distance was maintained by all group members. Dominance status may also affect spatial position in the group. Teichroeb and colleagues found that dominant vervet monkeys (*Chlorocebus pygerythrus*) maintained spatial positions in their social group which allowed them to consume more food than subordinate individuals. They observed higher-ranking males and females to travel and forage at the front, outside edge of the group, which may allow them to find food first and obtain more of it (Teichroeb et al., 2015).

Studies have shown that the distribution of food may also have a significant effect on aggression in species other than primates (Robb & Grant, 1977; Knapp et al., 2013; Vahl et al., 2005), such as fish, birds, and kangaroos among others. Spatial and temporal clumping of food have been shown to affect aggressive interactions in *Oryzias latipes* (Japanese medaka). Food that is temporally clumped elicits higher rates of aggression than food that is spatially dispersed (Robb & Grant, 1997). For a variety of species, the prevalence and magnitude of agonistic interactions and agonistic support is influenced by the temporal and spatial distribution of food resources, which has a profound effect on the patterns of dominance relationships among group members (Hill & Okayasu, 1995). Vahl et al (2005) demonstrated that, for ruddy turnstones (*Arenaria interpres*), an individual's dominance status and the spatial distribution of food effected the foraging success of individuals through an experiment that controlled food distribution and competitor presence. The authors suggested that dominant individuals may demonstrate more offensive behaviors when food is dispersed than when clumped. They claimed that when food is diminished, some subordinates may abstain from eating in order to avoid aggression from dominant individuals.

Animals living in habitats with diverse food distribution and predation risks are more flexible in their foraging strategies than animals living in habitats with fixed food distribution and steady rates of predation. Fission-fusion systems allow animals to respond to these variations in ecology. Animals forage with less contest competition by separating into smaller foraging groups. However, smaller foraging groups risk greater potential exposure to predators and threats from other hostile groups (Terborgh & Janson, 1986). Cohesion within baboon groups (*Papio*) is directly affected by such ecological factors (Barton et al., 1996). In baboon groups, grooming and the formation of coalitions appeared to be closely related to the levels of contest competition. When food was distributed in a more clumped way, that elicited high levels of WGC, and there were significantly different dominance, grooming, and coalitionary relationships than when it was distributed more evenly throughout the habitat. Fission also appeared to be directly affected by feeding competition in these groups. In baboons groups with little competition for food throughout their habitat, females formed fewer alliances, left their natal group with males, and formed new groups more often than occurred in groups with high levels of competition. Groups that fissioned often fused to form larger multi-male multi-female troops when ecological pressures favored larger groups (Barton et al., 1996).

Human Influences on Primate Habitats and Behaviors

Human influences change animal habitats. Some species may thrive in a wide variety of habitats, including disturbed ones, but many animals experience detrimental effects and avoid areas that have been altered by humans. Primates may develop new skill sets for retrieving resources when living in close contact with humans. Mangalam & Singh (2013) conducted a study in which *Macaca radiata* (Bonnet macaque) were presented with different novel food extraction tasks with varying degrees of difficulty. The authors found that macaques who spent

more time in closer proximity to humans and had more exposure to novel items were more successful at extracting food from multiple task items than macaques who lived in more isolated settings. Humans may have detrimental effects on primate populations by introducing new predators, such as dogs, and depleting a food resource that is important to the nonhuman primate species (Riley, 2007; Tsujino & Yumoto, 2014).

Human-provided food (hereafter, "human food") alters the behaviors of non-human primates in many ways. Ranging patterns and group size of primate groups living in anthropogenically altered environments may differ from those seen in wild populations (Albert et al., 2013; Altman & Muruthi, 1988, Berman et al., 2007; José-Domínguez et al., 2015; Koganezawa & Imaki, 1999; Riley, 2007, Sha & Hanya, 2013). When faced with habitat alteration that resulted in the depletion of all but one food resource, Riley (2007) found that *Macaca tonkeana* (Tonkean macaque) traveled less and maintained a smaller troop size compared to a troop of Tonkean macaques living in a habitat with little to no human influence. Some primates respond to habitat alteration by crop raiding to supplement their diet. Human crops often provide a high-nutrient food resource for non-human primates, which may be beneficial when other resources have been reduced. Crop raiding is a source of contention between humans and non-human primates, and humans often call for the extermination of non-human primates (Altmann & Muruthi, 1988; Knight, 2011; Radhakrishna et al., 2013; Riley, Tolbert, & Farida, 2013; Sha, Gumert, Lee, Jones-Engel, & Fuentes, 2009). This contentious issue is sometimes mitigated by provisioning the crop-raiding non-human primates and capitalizing on the troop as a tourist attraction (Knight, 2011).

Humans' actions may have a direct measurable impact on the behaviors displayed by other primates. The social interactions of *M. thibetana* who inhabit tourism sites are affected by

tourist activity. McCarthy and colleagues reported that tourists visiting the Valley of the Wild

Monkeys engaged in behaviors that appeared to be intended to evoke a reaction from the

macaques, such as railing slap. The study monkeys responded more to more intense behaviors

exhibited by tourists (see also Ruesto, Sheeran, Matheson, Li, & Wagner, 2010). Ruesto et al.

(2010) observed that tourist density had little to no effect on the threat levels of M. thibetana, but

higher decibel levels and the behaviors of tourists affected the rates of monkey threats. Long-

tailed macaques (*M. fascicularis*) in Singapore come into frequent contact with tourists and local

humans at forest edges. The macaques often interface with humans in relation to food and

sometimes took food directly from humans, which caused tension between human residents and

the monkeys in the region. Humans also fed the macaques, despite the fact that it is prohibited by

law. The most common factor motivating feeding is that humans felt the forest did not contain

enough food to sustain the monkeys (Sha et al., 2009).

Provisioning

Provisioning primate groups has been shown to alter the social interactions and

composition of affected groups. Primates exhibit higher levels of intra-group aggression while

foraging on human food compared to other food. Human food is often distributed in a more

clumped way than naturally-occurring food. Clumped food often elicits higher levels of contest

competition between individuals. Natural food is usually dispersed in a less clumped way that

allows primates to maintain a greater distance between individuals and avoid aggression

(Asquith, 1989; Fuentes & Gamerl, 2005; Hill & Okayasu, 1995; José-Domíngues et al., 2015;

Mori, 1977). Human food is often a high energy source that is easily digested, which monkeys

may value more highly than natural foods. Individuals respond to this type of food resource

either by kleptophagic tendencies (waiting until others are done and it is their turn), or aggression

(Fa, 1986). Hill and Okayasu (1995) observed a troop of Japanese macaques that was not provisioned and compared their data with results available for provisioned troops of Japanese macaques. The authors noted that agonistic interactions occurred more often in relation to foraging than any other activity, but agonistic interactions were observed at considerably lower rates in the non-provisioned troop than those reported for provisioned troops of Japanese macaques. They also found no evidence for "youngest ascendancy" (where younger individuals outrank the older offspring of their mother), which has been observed in provisioned troops (Hill & Okayasu, 1995).

Provisioning primates may have profound effects on their ranging patterns, activity budgets, and social interactions. Altmann and Muruthi (1988) found that *Papio cynocephalus* (savannah baboons) with access to human food spent less time feeding, and more time resting and socializing, than their non-provisioned counterparts. The authors also noted a decrease in home-range size and speed while traveling in semi-provisioned subjects. Subjects with a higher rank spent more time feeding on human food than subjects with a lower rank. Unwin & Smith (2010) observed two troops of *Macaca sylvanus* (Barbary macaques). One study troop was excluded from food provisions by the other study troop through BGC. The authors found that the excluded troop had a larger home range and devoted more time to foraging than the troop that monopolized the provisioned food. However, the troop that had access to the provisioned food continued to consume natural food and devoted more time to vigilance than did the other group. José-Domínguez et al. (2015) demonstrated that a troop of semi-provisioned pig-tailed macaques had ranging patterns and some behaviors that were more similar to those of territorial gibbons (*Hylobates lar*) than those of other, non-territorial groups of pig-tailed macaques. The semi-provisioned troop of pig-tailed macaques maintained a smaller home range, core area, and daily

paths than was seen in other groups of pig-tailed macaques. They also demonstrated more defensible behaviors than other groups of their species (José-Domínguez et al., 2015).

The home range of primate groups may be significantly altered by the presence of human food. Albert et al. (2013) found that pig-tailed macaques decreased their monthly home range in months when the macaques were forced to consume human food because fruit was less abundant. This finding was contrary to their prediction that the macaques would increase their home range in months that fruit was not abundant, and the authors believed that in the absence of human food the monkeys would have to travel further to find fallback foods (Albert et al., 2013). Sha and Hanya (2013) observed two troops of *Macaca fascicularis* (long-tailed macaques) that foraged on anthropogenic food, such as trash and tourist food handouts, but were not regularly provisioned. They were observed to maintain a large home range, which may be the result of the anthropogenic food being distributed unevenly in space and time. One of the two study groups consumed more human food than the other, and this group displayed a higher level of spatial dispersion while engaged in feeding activity. Both groups had a similar mean monthly dietary diversity (Sha & Hanya, 2013). Primates may subsequently fail to respond to other ecological factors. When faced with harsh winters primates who have altered their home range to gain better access to food from tourist do not always adjust their home range to find food from other sources than humans. The harsh winter can cause a decrease in tourists and the food supplements that they bring, which ultimately contributes to a decrease in troop size, because the troop cannot be sustained by the present nutrients (Koganezawa & Imaki, 1999).

Human food handouts may increase the amount of aggression received by subordinate group members. Self, Sheeran, Matheson, Li, Pelton, Harding, and Wagner (2013) found that when subordinate *M. thibetana* were given a food handout from a tourist they were at a higher

risk of receiving aggression from dominant males. The authors also found that the alpha and beta males engaged in the highest rates of infant-directed aggression, which was most common during provisioning times. However, despite this increased aggression, all individuals may still be able to consume equal amounts of food. Burwell (2013) observed the same group of *M. thibetana* who foraged on corn scattered by park rangers and concluded that all members of the study troop consumed similar amounts of corn. Rates of agonistic interactions directed at humans or other group members appeared to be correlated with food handouts from tourists, and were recorded more often in areas closer to tourists than those farther from tourists. Dominant individuals were more likely to monopolize the provisioning zones closest to viewing platforms through WGC. The park rangers scattered the corn in an effort to spread it evenly throughout the feeding site. However, food handouts from tourists usually occurred in a more patchy distribution than natural foods, which may force group members into closer proximity and increase levels of aggression (Burwell, 2013; Asquith, 1989).

Primates who live at tourist sites may direct aggression toward humans in an effort to obtain human food (Fuentes & Gamerl, 2005). Hsu, Kao, and Agoramoorthy (2009) reported higher levels of aggression within a troop of *Macaca cyclopis* (Formosan macaque) in relation to provisioned food. The authors also noted that aggression directed towards humans at Shou-Shan Nature Park, Taiwan was increased by human food. Interactions between humans and non-human primates could lead to the transfer of diseases between the species (Fuentes, 2006; Hsu et al., 2009). Macaques that live in habitats with a large human presence are considerably more likely to interact with humans when human food is present as opposed to when it is absent (Fuentes, Kalchik, Gettler, Kwiatt, Konecki, & Jones-Engel, 2008). Macaques display higher

rates of aggression toward humans when tourists attempt to feed them, which places both species at a higher risk of disease transmission (Fuentes, 2006).

Primates who live near human food and frequently rely on it have higher levels of WGC, thus they exhibit higher levels of aggressive behavior (Asquith, 1989; Fuentes & Gamerl, 2005; Hill & Okayasu, 1995; José-Domíngues et al., 2015; Mori, 1977). This is true because the distribution of food has such a large effect on group structure. The defensibility, nutrient intake, and distribution are factors that determine if individuals compete more or less intensely. Food that is not easily defended does not create high levels of WGC. Food that is distributed in a more clumped manner also draws primates into closer proximity which may lead to higher rates of aggression. Food that is less valued, due to low nutrients or high availability, does not need to be defended as much as food that is of higher value (Furuichi, 1983; Hanya, 2009; Mori, 1977; Shopland, 1987; van Schaik, 1989; Vahl et al., 2005). Human food provisions are typically distributed in a more defensible way and often contains higher nutrients (Asquith, 1989; Mori, 1977; Fa, 1986; José-Domínguez et al, 2015; Orams, 2002 Riley, Tolbert, & Farida, 2013). Some may attempt to lower the aggression directed towards them by engaging in affiliative behaviors, such as grooming, while resting with other group members (Barrett et al., 1999; Carter et al., 2009; Seyfarth, 1977; Silk et al., 2010; Tiddi et al., 2011). For all of these reasons macaques who inhabit a tourism site which provisions them with human food will likely exhibit higher levels of aggression and submission while in areas with human food and higher levels of affiliative behaviors while in areas with little to no human food while resting. They would also presumably maintain a closer proximity while in relation to human food than while in areas with no human food.

Macaques

Primatologists classify 23 species within the genus *Macaca,* organized into several different lineages of semi-terrestrial Old World monkeys who often live in multi-male multi-female groups (Campbell, Fuentes, Li, Zhao, & Fan, 2015; Campbell, Fuentes, MacKinnon, Panger, & Bearder, 2007; Thierry, 2011). Compared to other monkeys, macaques range in size from medium to large, have a heavy build, and vary in color between different shades of brown and black. The *Macaca* genus occurs in a variety of habitats throughout Asia and Africa. Given the diverse habitats inhabited by macaques, it is not surprising that they appear to have an adaptable diet but are primarily frugivorous (Campbell et al., 2007; Fooden, 1982; Thierry, 2011; Riley, 2007; Thierry, 2011). Most macaque species exhibit male dispersal into neighboring groups, and groups share overlapping home-ranges.

Males often hold a variety of dominance statuses depending on their competitive abilities during their lifespan, while the dominance rank of female macaques is often stable and dependent on kin-based alliances (Thierry, 2011). Thierry (2000) established a grading system of macaque dominance styles classifying species with strict hierarchies as despotic and others as relaxed. Thierry's classifications include four proposed grades of despotism. Grade one includes species that demonstrate high levels of despotism. Characteristics of this grade include low tolerance, strong kinship bonds among females, asymmetric conflict, low levels of reconciliation and affiliation, and mothers do not allow others to handle infants often. Grade four is the opposite of grade one and species in classified in this grade are considered relaxed. They are more tolerant, reconcile more often, have bidirectional conflict, and affiliate more often. Despotic species exhibit high levels of competition for all resources, and relaxed species exhibit lower levels of competition for all resources (Thierry, 2000; Thierry et al., 2000).

M. thibetana is one of the largest species within the genus, and adult males were often larger that adult females. *M. thibetana* is classified into the *sinica* lineage. They inhabit broadleaf, evergreen forests of east-central China, which have become fragmented due to human influences (Deinard & Smith, 2001; Fooden, 1982; Morales & Melnick, 1998; Zhang et al., 1981). Little information is available on the natural diet of this species, because research has been limited to tourist sites. Much of the information available on the species comes from two sites: Mt. Emei, China (e.g., Deng & Zhao, 1991) or Mt. Huangshan, China (e.g., Berman et al., 2004). Macaque groups at both sites have been and continue to be provisioned in order to draw them closer to researchers and tourists (Matheson, Sheeran, Li, & Wagner, 2006; Ogawa, 1995; Usui et al., 2014; Zhao, 1993).

The degree of despotism exhibited by *M. thibetana* has been difficult to classify (Balasubramaniam et al., 2012; Berman et al., 2004; Berman, Ionica, Dorner, & Li, 2005; Berman et al, 2006). The latest classification places *M. thibetana* in grade scale two on Thierry's grade scale of despotism (Balasubramaniam et al., 2012). Berman, Ionica, and Li (2004) found that *M. thibetana* exhibit a linear dominance hierarchy, males outrank females, and the female hierarchy has a weak kin bias. Males engage in intense aggressive competition during the mating season, which often leads to injuries and may cause younger males to leave the troop in which the aggressive interaction occurred (Zhao, 1994). Lower-ranking group members remain on the periphery of the troop and avoid higher-ranking group members during the mating season. Dominant males and females are more aggressive towards subordinate group members during the mating season, and even disrupt sexual encounters involving subordinate individuals (Zhao, 1993). High-ranking males co-feed more often with lower-ranking males who support them in agonistic interactions than they co-feed with lower-ranking males who do not support them.

Males often engaged in reciprocal coalitions which may eventually lead to rank reversals in some cases (Berman, Ionica, & Li, 2007). .

Berman, Ogawa, Ionica, Yin, & Li (2008) demonstrated that the grooming networks of females is partially effected by time constraints. When group sizes are larger, subjects spend longer periods of time grooming fewer individuals. Groomees, are often closely related kin. However, grooming rates are similar in all group sizes and competition within the group appears to have little effect on grooming rate or network (Berman et al., 2008). Both males and females have been observed to use grooming as a social tool. Males who rank lower in the hierarchy groom more dominant males, presumably to gain a higher-ranking ally (Xia, Li, Garber, Matheson, Sun, & Zhu, 2013). Female *M. thibetana* preferentially groom and form reciprocal grooming relationships with related and similarly-ranked group members (Xia, Li, Garber, Sun, Zhu, & Sun, 2012). *M. thibetana* often have high levels of affiliation after aggression, and male-male dyads often reconcile by embracing or engaging in social mounts (Berman et al., 2005).

M. thibetana at Mt. Huangshan, China have been provisioned and observed since 1986 (Berman & Li, 2001). The monkeys were relocated, for purposes of tourism, and their range was restricted several years after the provisioning began. The translocation of the troop affected the group's ability to recruit new group members for at least three years following the relocation, and recruitment rates did return to normal until the fourth year following the relocation. There were also high rates of infant mortality in the years following the group relocation, which may be due in part to the range restriction of the troop (Berman & Li, 2001). Berman, Li, Ogawa, Ionica, and Yin (2007) postulated that infant mortality was the result of range restriction, because range restriction appeared to cause higher rates of aggression directed toward infants, as well as other group members, which may lead to infanticide. Wescliff (2012) demonstrated that *M. thibetana*

maintained a greater distance while foraging than when resting or traveling. When the monkeys were provisioned the number of neighbors at more distant proximities increases. No kin bias was observed, but subjects appeared to prefer close proximity with other individuals of similar rank (Wescliff, 2012). While studying collective movements, Wang, Sun, Li, Xia, Sun, and Zhang (2015) found that *M. thibetana* follow the group when a quorum of seven individuals is moving and that individuals are more likely to follow group members with whom they have an affiliative relationship. The study group also appears to be more relaxed outside of provisioning zones.

The park rangers at Mt. Huangshan exhibit a variety of management styles. Despite the differences in management styles, levels of monkey aggression directed toward other group members and their self-directed behaviors remained constant (Usui et al., 2014). Higher-intensity behaviors were directed toward tourists who attempted to feed the macaques. This was encouraged by some rangers, who sometimes provided corn for tourists to distribute and was discouraged by other rangers, who confiscated food tourists brought to feed monkeys. Young and adolescent members of the YA1 troop spend more time near the platforms during non-feeding times and adults are observed near the platforms more often at feeding times, which effects priority of access. Agonistic behavior by more dominant individuals appear to follow a pattern of adult monkeys threatening juveniles and juveniles then threatening humans. Although human densities had little effect on the monkeys' threat rates, anecdotal reports provide evidence that tourist interactions may affect monkey-monkey aggression rates (Matheson et al., 2006).

Previous research has demonstrated that tourism affects the social interactions of *M. thibetana* (Berman et al., 2007; Berman & Li, 2001; 2007; Matheson et al., 2006; Ruesto et al., 2010). *M. thibetana* have been shown to maintain strict hierarchies that are similar to those of despotic species but they also exhibit some social behaviors similar to those of species with more

relaxed hierarchies (Balasubramaniam et al., 2012). It is possible that the presence of human food inflates the agonistic and aggressive behaviors of *M. thibetana* at the tourism sites in which they are studied (Asquith, 1989; Mori, 1977; Fa, 1986; José-Domínguez et al, 2015; Orams, 2002; Riley, Tolbert, & Farida, 2013). Human food may also bring the monkeys into closer proximity than food existing more naturally throughout the forest (Furuichi, 1983; Hanya, 2009; Mori, 1977; Shopland, 1987; van Schaik, 1989; Vahl et al., 2005). *M. thibetana* have also been shown to maintain a grooming networks (Berman et al., 2008). These grooming networks may help to lower the amount of aggression directed towards subordinate individuals (Barrett et al., 1999; Stammbach & Kummer, 1982; Tiddi et al., 2011).

The literature on foraging and anthropogenic environments shows that non-human primates are affected by alterations of food distribution made by humans. This led me to pose questions about the influences of human food on *M. thibetana* at a tourist site. The first question was, does the presence of human food alter the social behaviors within the group of *M. thibetana*. I then asked whether the presence of human food alters the inter-individual distance of the group. I hypothesize that *M. thibetana* will exhibit different levels of agonistic, submissive, and affiliative behaviors in provisioning zones than in non-provisioning zones. I predict that levels of agonistic and submissive behaviors will be higher in the provisioning zones and levels of affiliative behaviors will be higher in non-provisioning zones. I hypothesized that subjects will maintain a different inter-individual distance while in the provisioning area than while in non-provisioning areas and predicted that subjects will maintain closer proximity in the provisioning zones than non-provisioning zones.

CHAPTER III

METHODS

Subjects and Study Site

The current study was conducted at Mt. Huangshan, China. Mt. Huangshan is a

UNESCO World Heritage Site and contains peaks of evergreen and deciduous forests. The

Valley of the Wild Monkeys (VWM) is a tourist destination in the Huangshan Scenic District.

Monkeys are provisioned with corn at VWM to draw them closer to tourist platforms (Berman,

Li, Ogawa, Ionica, & Yin, 2007; Burwell, 2013; Ruesto et al., 2010). The site has been divided

into six provisioning zones, which include flat grassy areas near the tourist viewing platforms

(zones 1 and 2), rocky hills (zone 3) rocky uneven terrain with cliffs, pools, and streams (zone

4), a flat area with few rocky areas (zone 5), and cliffs with waterfalls (zone 6) (Matheson,

Sheeran, Li, & Wagner, 2006; Burwell, 2013). Tourists are confined to platforms from which

they view the monkeys being fed in the provisioning zones.

The monkeys are provisioned with corn daily, which provides the group with

approximately 5kg of corn a day (Burwell, 2013). Park staff attempt to scatter the corn across the

six provisioning zones in an effort to distribute the corn evenly among the monkeys. However,

corn may not reach some of the further zones and may fall down uneven terrain and cluster in

some spots. Signs and park staff interventions discourage tourists from feeding the monkeys, but

some still do (Burwell, 2013; Usui et al., 2014). The study subjects were members of the

Yulingkeng A1 (YA1) troop at the time of data collection. The YA1 troop is habituated to

human presence and included roughly 42 individuals at the time of data collection: 8 (19% of the

group) adult males, 12 (29% of the total group) adult females, 5 (11% of the total group)

subadult males and females, 10 (24% of the total group) juvenile males and females, and 7 (17% of the total group), and infants (Wang Xi, 2015 personal communication to Schnepel).

Procedures

I collected data from 17 August-18 September 2015. I used camera traps set in provisioning and non-provisioning sites to obtain data on how provisioned food may alter the behaviors of *M. thibetana*. I sorted and coded videos upon returning to Central Washington University. I recorded all occurrences of foraging while at the monkey park, the identity of the subject, location (provisioning or non-provisioning zone), food type (natural, e.g., leaf; human, e.g., rice puff bar), date and the identities and behaviors of individuals in proximity to one another.

I recorded data using 60-second all occurrence sampling (Altmann, 1974) from videotaped data collected from camera traps. I recorded all occurrences of agonistic, submissive, and affiliative behavior according to an amended ethogram developed by Berman, Ionica, & Li, (2004). I added three affiliative behaviors to the ethogram. Those three behaviors are; Bridge: "A complex sequence of behavior in which an individual approaches another alternating glances at the receiver and an infant that is carried by either the approacher or the approached. The pair holds the infant between them and simultaneously lick the infant's genitals or body while teeth-chattering vigorously" (Ogawa, 1995). Play: "Repeated, incompletely functional behavior differing from more serious versions structurally, contextually, or ontogenetically, and initiated voluntarily where the animal is in a relaxed low-stress setting" (Burghardt & Sutton-Smith, 2005, p.82). Cling: Adult/sub-adult/ juvenile, and/or infant hold, carry, or hang on to one another. I also added one behavior to the aggressive behaviors, which is; Display: exaggerated branch or object shaking, jumping, or other motions directed at group or individual often without

vocalization but may include grunting or other aggressive vocalizations. I used scan samples (Altmann, 1974) taken at 15-second intervals and recorded the number of individuals, proximity, age/sex class of individuals, and general location of the foraging group were recorded. I recorded the number of individuals by counting the visible individuals in a frame. I defined proximity as individuals within arm's length. I did not record those who were outside of arm's length as in proximity.

It was not possible to reliably record identities of individuals from video data. Therefore, I recorded the age/sex class of individuals following the criteria of Xia et al. (2012) when possible. I found that the average total number of males per scan was 0.35, females was 0.56, subadults was 0.16, juveniles was 0.45, infants was 0.24, unknown (age) males 0.003, unknown (age) females 0.002, unknown adults was 0.04, and unknown subjects was 0.18 for the provisioning zone. The age/sex classes are represented proportionately when the group composition is considered. Grooming and proximity were recorded separately. Grooming was recorded in the all-occurrence samples while proximity was recorded in the scan samples. There were times when individuals who were recorded as grooming in the all-occurrence samples were also recorded as in proximity in the scan samples (Altmann, 1974). I noted the location as the camera number since the locations of the different cameras were mapped and recorded. The cameras only allowed a limited frame and it is possible that behaviors occurred outside of the frame by subjects from any age/sex class that were unable to be captured in the data because of the limited frame of the video footage. The limited frame may have also been an advantage because it allowed for unbiased sampling. The samples captured by the cameras were at random when an individual moved in front of the camera, therefore I was unable to choose the data captured. This allowed me to collect unbiased data.

I placed trail-cameras at six known (based on previous research by Anhui University and CWU faculty) feeding sites throughout the forest at non-provisioning areas, at provisioning zones, and at an intermediate zone (between the provisioning zone and the forest) at Mt. Huangshan, China. I placed two cameras ~18 m apart in provisioning zones where the YA1 troop is fed. I placed three cameras 5-10 m apart on a forested slope. I placed one camera in an intermediate area between the provisioning zones and the forest. During the first week I removed the camera memory cards every evening and reviewed the videos to ensure that the trap locations would provide video footage of monkeys. I moved the cameras if video footage from a particular site recorded few to no videos of the study troop. Camera placement began on August 4 and all camera traps remained stationary from 17 August to18 September 2015. I checked the cameras every one to eight days at which time I checked battery life, memory cards were changed, and date and time stamp as well as settings were checked for accuracy. I set the six camera traps to record 60 second videos when triggered, and each camera triggered within one second of movement (Gerber et al., 2014; Farris et al., 2014; Loken et al., 2013). The video recordings were automatically date and time stamped. I screened data from the camera traps for monkey presence on days when cameras were checked. I sorted the videos into six categories within their camera location upon returning to CWU. The video categories were camera investigation, foraging, miscellaneous, night, poor quality, and social behavior. After sorting, I scored 600 videos for monkey behaviors and proximities.

Using a random number generator, I randomly selected previously coded video footage gathered from the camera traps in which a wide range of ethogram behaviors were exhibited. I used this footage to test intra-observer reliability. I coded 35 videos that I had coded for the study a second time for social behavior and proximity, with a score of ≥85 acceptable for

ethogram behaviors and proximity. I passed the intra-observer reliability with 100 percent accuracy for social behaviors, 98 percent accuracy for proximity, and 97 percent for age/sex classification.

The camera traps yielded a total of 7,942 videos with macaques visible. There were 4,539 foraging videos (27 from the forest, 4,489 from the provisioning zone, and 23 from the intermediate area). The cameras recorded 701 videos of monkeys' social behavior (105 forest, 320 provisioning zone, and 276 intermediate area). There were 1,450 videos with miscellaneous behaviors (153 from the forest, 1,115 provisioning zone, and 182 intermediate area). Camera investigation by monkeys was captured in 604 videos (321 forest, 102 provisioning zone, and 181 intermediate area). There were also 648 poor quality videos (forest 137, 409 provisioning zone, and 102 intermediate).

I randomly selected 600 videos from the categories of foraging, social behavior, and miscellaneous categories from provisioning and non-provisioning zones and coded them using the data coding methods outlined above. While coding the videos it was assumed that all animals could be in any location at any time therefore I treated all samples as independent. I conducted a total of 600 all-occurrence samples for behavior and a total of 2,998 scan samples for proximity. Scans with no monkeys visible were excluded from data analysis. The average number of individuals in proximity per scan was calculated in Excel by dividing the total number of individuals in proximity per scan by the total number of individuals visible in that scan. The proximity data was aggregated for all age/sex classes. This was done in order to understand determine the effects that human food has at the group level. Similarly, the behavioral data was aggregated by category into either agonistic, submissive, or affiliative behaviors in order to determine the effects that human food has on the overall behavioral categories rather than

individual behaviors. I used *R-statistics* to perform a Shapiro-Wilk Test for Normality. Once

normal distribution was determined I performed a *t* test for behaviors and proximity in *R-*

statistics. I set alpha at 0.01 for all tests.

CHAPTER IV

RESULTS

I determined that data on agonistic behaviors was normally distributed (non-provisioning $W = 0.13$, $p < 0.01$; provisioning $W = 0.34$, $p < 0.01$). I found a significant difference in agonistic behaviors in provisioning zones and non-provisioning zones ($N = 600$ scans, $t = -5.61$, $df = 389.38$, $p < 0.01$). There were more agonistic interactions in the provisioning zones (average $= 0.20$) than in the non-provisioning zones (average $= 0.04$).

I determined that data on submissive behaviors was normally distributed (non-provisioning $W = 0.16$ $p < 0.01$; provisioning $W = 0.43$, $p < 0.01$). I found that there was a significant difference in submissive behaviors in the provisioning zones and non-provisioning zones ($N = 600$ scans, $t = -4.94$, $df = 385.77$, $p < 0.01$). There were more submissive behaviors in the provisioning zones (average $= 0.40$) than in the non-provisioning zones (average $= 0.07$).

I determined that data on affiliative behavior was normally distributed (non-provisioning $W = 0.75$, $p < 0.01$; provisioning $W = 0.66$, $p < 0.01$). I found a significant difference in affiliative behaviors in the provisioning zones and non-provisioning zones ($N = 600$ scans, $t = 2.52$, $df = 592.16$, $p < 0.01$). There were more affiliative behaviors in the non-provisioning zones (average $= 0.84$) than in the provisioning zones (average $= 0.62$).

For proximity data the average number of subjects in proximity per scan was put into R and a t test was completed on those averages for the provisioning zones and non-provisioning zones. I determined that proximity data was normally distributed (non-provisioning $W = 0.73$ $p < 0.01$; provisioning $W = 0.62$, $p < 0.01$) I found that there was a significant difference in proximity between the provisioning zones and the non-provisioning zones ($N = 2382$ scans, $t = 16.17$, $df = 1916.26$, $p < .01$). I found that more subjects are in proximity while in non-

provisioning areas (average = 0.42) compared to the provisioning sites (average = 0.20). To determine if the intermediate zone skewed the results I separated the forest data and intermediate zone data and performed further t tests. I determined that all proximity data was evenly distributed (provisioning $W = 0.62$, $p < 0.01$; forest $W = 0.64$ $p < 0.01$; intermediate $W = 0.75$, $p < 0.01$). The results showed that there was a significant difference in proximity between the forest, intermediate, and provisioning areas (forest & intermediate $N = 1129$ scans, $t = -5.61$, $df = 739.55$, $p < 0.01$; forest & provisioning $N = 1620$ scans, $t = 6.01$, $df = 471.40$, $p < 0.01$; provisioning & intermediate $N = 2004$ scans, $t = 16.17$, $df = 1916.26$, $p < 0.01$). I found that proximity was highest in the intermediate areas (average = 0.50) and second highest in the forest (average = 0.31) and lowest in the provisioning areas (average = 0.20).

CHAPTER V

DISCUSSION

My results show that human food alters the social behaviors and proximity of *M. thibetana*. The video footage also shows that camera traps are an effective way to collect data on provisioned monkeys. However, it may be best to collect data using a combination of camera traps and direct observational methods (Lhota et al., 2012). Camera placement is also important to consider (Gerber et al., 2014; Loken et al., 2013; Pebsworth & Lafleur, 2014). The cameras for this study were moved several times, but I may have captured more of the desired foraging videos if I had made a few more adjustments. It is also important to note that the monkeys continued to investigate the cameras until the end of the study, which suggests that they may never become truly habituated to them. I found that more than half of the videos from the forest were camera investigation. I also anecdotally observed monkeys investigate a metal box that had been in their environment since before data collection began, which provides further evidence that the subjects may not habituate to novel human objects in their environment.

My first hypothesis, which states that *M. thibetana* will exhibit different levels of social behaviors in provisioning zones than in non-provisioning zones, was supported by the data. The prediction that levels of agonistic and submissive behaviors will be higher in the provisioning zones was also supported. I also predicted that affiliative behavior would be higher in the non-provisioning zones, which was supported by the data. The data revealed that *M. thibetana* display higher amounts of agonistic and submissive behaviors in the provisioning zones compared to non-provisioning zones, as expected from literature on foraging. Human food is often of higher value to non-human primates than is natural food, because the former food type is more nutrient rich and easier to digest. Food that is more highly valued often elicits higher levels

of WGC (Asquith, 1989; Hill & Okayasu, 1995; Hsu et al., 2009; Mori, 1977; Fa, 1986; Janson, 1985; José-Domínguez et al, 2015; Orams, 2002; Riley et al., 2013; van Schaik, 1989). Even macaque species such as Japanese macaques that are usually considered to be a grade one on Thierry's scale of despotism have been observed to exhibit lower rates of aggression when not provisioned with human food (Hill & Okayasu, 1995; Thierry, 2000). The exaggerated WGC may raise the levels of both agonistic and submissive behaviors. High levels of agonism appear to elicit high levels of submission which could be a way of avoiding aggression (Barton et al., 1996; Koenig, 2002; van Schaik, 1989; van Schaik & van Noordwijk, 1988; Teichroeb et al., 2015; Vahl et al., 2005; Vogel & Janson, 2007).

The data that I gathered by direct observation recorded that the subjects frequently received food from tourists. The possibility of food handouts from tourists may have exaggerated the levels of aggression (Fuentes & Gamerl, 2005; Self et al., 2013). Self, Sheeran, Matheson, Li, Pelton, Harding, and Wagner (2013) reported that high ranking *M. thibetana* at the same study site exhibited higher rates of aggression when tourist food handouts occurred. The handouts from tourists are often more clumped and are distributed randomly. Monkeys who competitively exclude other group members from provisioning zones where tourists may toss food have a higher chance of receiving food. Teichrobe, White, and Chapman (2015) also found that dominant Vervet monkeys maintained positions at the front of the group while moving, which allowed them to find and access food patches first. It is possible that some individuals exhibited higher rates of aggression and remained in the provisioning zones more often than did other individuals; however, identities of subjects were not recorded. I was interested in determining overall changes in social behavior for all group members in aggregate, not individual changes in social behavior. Individuals in dominant positions presumably exhibit higher rates of aggression

and are able to remain in preferred locations like the provisioning zones (Asquith, 1989; Fa, 1986; Fuentes & Gamerl, 2005; José-Domínguez et al, 2015; Hill & Okayasu, 1995; Matheson et al., 2006; Orams, 2002; Unwin & Smith, 2010; Self et al., 2013; Teichroeb et al., 2015).

Macaca thibetana at Mt. Huangshan participate in more affiliative behaviors outside of the provisioning zone than they do in the provisioning zone. This agrees with the literature. Subordinate animals often engage in grooming as a way to gain tolerance and support from more dominant group members (Barrett et al., 1999; Carter et al., 2009; Seyfarth, 1977; Silk et al., 2010; Tiddi et al., 2011). Carter, Macdonald, Thomson, and Goldizen (2009) reported that in grey kangaroos (*Macropus giganteus*) female group members were able to forage for longer if they regularly associated with certain group members. The affiliative behaviors occurring at my site outside of the provisioning zones could be used by the lower-ranked group members to gain tolerance while foraging on human and natural food. They could also use these interactions as a way to gain support from dominant individuals in their next agonistic encounter (Seyfarth, 1977; Silk et al., 2010). Grooming is more likely to occur when animals are more relaxed, which could be the reason the YA1 troop of *M. thibetana* were observed to groom more often in the non-provisioning zones. They have been found to be more relaxed in non-provisioning zones (Wang et al., 2015).

The second hypothesis, which states that subjects will maintain a different inter-individual distance while in the provisioning area than while in non-provisioning areas, was supported. However, my prediction that subjects would maintain closer proximity in the provisioning zones was not supported. In fact, my data show that the opposite is true. *M. thibetana* at Mt. Huangshan maintained a closer proximity in the forest than they did in the provisioning zones. To determine if the intermediate area skewed the results I separated the

forest zone data and reran my analysis. My data showed that the subjects remained in closer proximity in the intermediate area than in the forest or in the provisioning zone. It also showed that the subjects are in closer proximity in the forest than in the provisioning zones.

At first glance this finding was surprising, but after reviewing the literature it is less surprising for many reasons. The first of those reasons is that at Mt. Huangshan the park staff attempt to distribute the corn in a more widely dispersed, manner (Burwell, 2013). This goal appears to have been attained, and the monkeys are able to maintain a greater inter-individual distance. The second reason that the monkeys may be maintaining a greater inter-individual distance is that they may be using kleptophagic tendencies while foraging. Individuals who are more likely to receive aggression in the provisioning zone may stay outside of the provisioning zones and wait until the individuals more likely to aggress toward them consume their food provisions and move on (Fa, 1986; Janson, 1985). Janson (1985) found that subordinate brown capuchins would go hungry before risking aggression directed towards them from feeding dominant individuals. Burwell (2013) also found that *M. thibetana* at Mt. Huangshan move into the provisioning zones in turns that begin with the most dominant individuals and end with younger and less dominant individuals.

The unexpected proximity pattern could also be due to the social behaviors that occur in the different zones. There is an increased level of affiliation in the non-provisioning zones compared to provisioning zones. Affiliative behaviors, such as grooming, often last longer than aggressive behaviors. Primates often move back to the tolerance distance when aggression is directed towards them, thus moving out of close proximity (Furuichi, 1983; Janson, 1985; Shopland, 1987). The subjects appeared to use the intermediate area as a place to engage in social behavior while still monitoring the provisioning zones for food. Human food is mostly

absent from the intermediate area and park staff seldom enter that area. The intermediate area may therefore be a place that the monkeys use to socialize while waiting for human food. The intermediate zone may also be beneficial for the humans who visit the park because they can still view the monkeys with reduced contact between macaques with tourists and park staff. The reduced contact reduces the risk for disease transmission between humans and monkeys (Fuentes, 2006; Hsu et al., 2009).

Conclusions and Implications for the Future

The findings of this study indicate that using camera traps to study foraging behaviors is feasible but may need to be aided by the collection of other, more direct, observational data. My study results also indicate that the rates of agonistic and submissive behaviors are exaggerated in non-human primates when they are provisioned with human food. Staff at tourism sites, such as Mt. Huangshan, may need to explore strategies for mitigating the high levels of within-group competition that surrounds human food. One of the strategies that may have an impact on *M. thibetana* at the Valley of Wild Monkeys is to prohibit tourists from bringing food of any kind to the platforms. Future studies could work to identify all of the factors that occur prior to the monkeys' agonistic behaviors and find ways to decrease those that appear to contribute to increased aggression. I found some positive aspects of the management style at VWM. One of those aspects was an expansion on previous findings: the methods used by park staff to distribute corn evenly throughout the provisioning zones appears successful in allowing the monkeys to maintain greater inter-individual distances. The other, more surprising, positive aspect of VWM is that the intermediate area is useful to all who visit and inhabit the monkey park. It may be beneficial to create and maintain a larger intermediate area both at the Valley of the Wild monkeys and at future macaque tourism sites.

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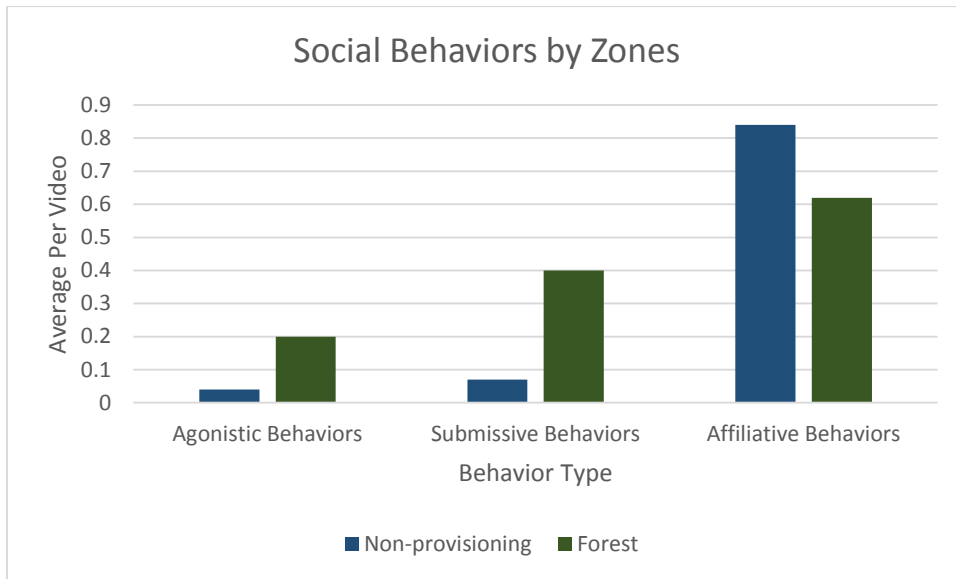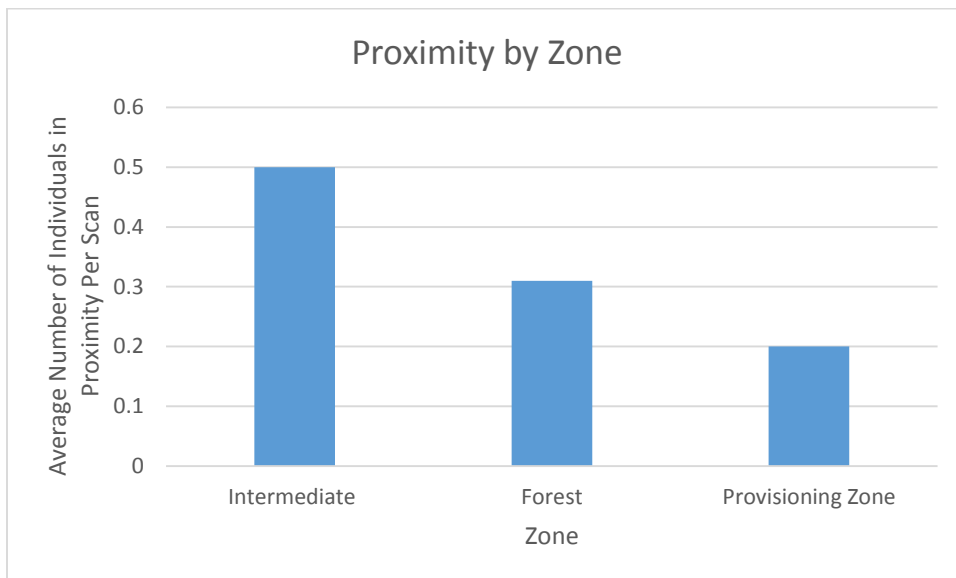
APPENDIXES

APPENDIX A

SOCIAL BEHAVIORS AND PROXIMITY GRAPHS

Figure 1: Social Behaviors by Zone

Figure 2: Proximity by Zone