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Group Differences in Mother-Infant *Macaca fascicularis* Behavior, Parasite Load, and Body Condition within an Anthropogenically Altered Forest

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GROUP DIFFERENCES IN MOTHER-INFANT *MACACA FASCICULARIS* BEHAVIOR, PARASITE LOAD, AND BODY CONDITION WITHIN AN ANTHROPOGENICALLY ALTERED FOREST

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Master of Science

Primate Behavior and Ecology

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by

Elizabeth M C. Coggeshall

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ABSTRACT

GROUP DIFFERENCES IN MOTHER-INFANT *MACACA FASCICULARIS* BEHAVIOR, PARASITE LOAD, AND BODY CONDITION WITHIN AN ANTHROPOGENICALLY ALTERED FOREST

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This study aimed to establish preliminary health and behavioral data, as well as understand group variation for a large population of *Macaca fascicularis* individuals within an anthropogenically altered monkey forest. A parasitic analysis of 40 mother and infant individuals showed that *M. fascicularis* carried 13 different parasitic taxa, and that there was parasitic variation between groups. Body condition scores were determined using a newly created and adapted body condition scale from 146 sampled mother macaques. Body condition scores were significantly different between groups, specifically the pond group when compared to the three other groups. Mother-infant behavioral differences were seen between every group of macaques. Health and behavioral variations are likely influenced by the high population density, contaminated food and water sources, human activity, or unquantifiable variables such as age and rank.

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CHAPTER I

INTRODUCTION

Human-primate conflict has only increased as deforestation rates increase and primates lose their natural habitat (Estrada et al., 2018). The consequences of natural habitat loss for primates include increased crop-raiding and urban encroachment, increased disease transmission, behavioral changes, and fluctuations in the roles primates play in cultural contexts (Brotcorne et al., 2014; Campbell-Smith et al., 2010; Chi Mun Sha et al., 2009; Fuentes, Southern, & Suaryana, 2005; Peterson, Riley, & Putu Oka, 2015; Radhakrishna, 2018). Many cultures and religions hold monkeys in a high or holy regard and even provision them (Chi Mun Sha et al., 2009; Peterson et al., 2015). This can be seen in multiple religions such as Buddhism, Hinduism, and Shintoism. For example, the Hindu perspective that macaques are spiritually powerful is reflected in the maintenance of populations of *Macaca fascicularis* (long-tailed macaques) at temple sites in Bali, where locals protect, provision, and promote this species to show their philosophy of health, happiness, and prosperity. It is interesting to note that the term “sacredness” was not introduced into this area until western colonization, but the positive treatment of the macaques stretches back before these colonialist times (Peterson et al., 2015). This positive perspective of macaques, who are often seen as godly mediators, is prevalent in other countries, such as Thailand, and can facilitate the study of primates in close proximity with minimal agonistic threats from humans (Radhakrishna, 2018). I had such an opportunity to study *M. fascicularis* at a temple site in Phana, Thailand in the religiously affiliated Don Chao Poo Forest.

In this study, I examined mother-infant behaviors and collected fecal samples that were assessed for gastro-intestinal parasites. I aimed to assess how anthropogenic effects could impact group differences in mother and infant parasite load, body condition, and behavior. Macaques are excellent study subjects to understand behavioral complexities because they live in large groups and are highly social. In addition, macaques are appropriate subjects to understand parasitic threats because they experience high levels of human conflict, live in anthropogenic habitats, and their sociality promotes the likelihood of parasite transmission between individuals (Hussain, Ram, Kumar, Shivaji, & Umpathy, 2013; MacIntosh et al., 2012).

CHAPTER II

LITERATURE REVIEW

Macaque Natural History

The members of subfamily Cercopithecinae range across Asia and Africa and include the tribes Cercopithecini and Papionini. The tribe Papionini contains *Macaca, Lophocebus, Rungwecebus, Papio, Theropithecus, Cercocebus,* and *Mandrillus.* The genus *Macaca* contains 23 recognized species (see Table A1 for species diversity within the *Macaca* genus) (Brandon-Jones et al. 2004; Thierry, 2007). *Macaca* became distinct from Papionini approximately 9-10 million years ago (mya), and fossil data indicate that the first *Macaca* lineage appeared 7 mya in Africa and the next appeared in Asia approximately 5.5 mya (Delson, 1980). Current *Macaca* diversity stems from three ancestral lineages (*silenus-sylvanus, sinica-arctoides,* and *fascicularis-mulatta*) that diverged from the ancestral Asian stock approximately 4.32 mya (nuclear genes and mitochondrial genome, Jiang et al., 2016; Thierry, 2007) with *M. fascicularis* became distinct from the *fuscata-mulatta* ancestral stock at 1.79 mya. Extant examples of the *fascicularis-mulatta* lineage include four species: *M. fascicularis, M. mulatta, M. fuscata,* and *M. cyclopis* (Thierry, 2007). Phylogenetic and geographic information of the three ancestral lineages of extant *Macaca* provides insight into when and how they taxonomically diverged and dispersed across Asia (Thierry, 2007).

Macaque distribution and diet

Macaca is found in a broad geographic area from Northern Africa and Gibraltar to Afghanistan, Pakistan, Southeast Asia, Malaysia, and Japan. Their environments are vast and vary from semi-desert landscapes, deciduous forests in mountain ranges, tropical forests, mangrove swamps, and urban environments (see Table B1 for long-tail macaque environment diversity) (Gumert, 2011).

M. fascicularis is one of the most widely distributed species and is found across Southeast Asia in Bangladesh, Myanmar, Thailand, Cambodia, Laos, Vietnam, Malaysia, and the Philippines. In concurrence with their wide and varied distribution, *M. fascicularis* also live in a variety of natural environments, such as tropical rainforests and inland wetlands, and anthropogenically altered, urban, and artificial areas, such as laboratories (Sha & Hanya, 2013).

Macaca species have diverse and flexible diet that include fruits, seeds, flowers, leaves, shoots, bark, smaller vertebrate prey, and insects, and they are frequently referred to as generalists with great dietary plasticity (Sha & Hanya, 2013). Macaques that live in tropical forests tend to be more frugivorous with a higher diversity in their food choices, whereas macaques in temperate areas, such as Japan, focus their diets more on leaves and seeds (Thierry, 2007). In environment's with increasing human population pressures, macaques have started to incorporate human food into their diet, such as cultivated plants or discarded human foodstuffs (Sha & Hanya, 2013; Fuentes et al., 2008). Specifically, *Macaca fascicularis* is defined as being an opportunistic omnivore (Gumert, 2011). *M. fascicularis* flexible diet allows them to more easily inhabit a variety of environments, including urban settings and anthropogenically altered areas.

Many humans provision macaques because of religious or scientific motivations. Provisioned food usually consists of grains and fruit that are abundant in the local area and are energy-rich (Fuentes et al., 2011; Saj, Sicotte, & Paterson, 1999). Specifically, in Bali, temple staff have been documented to provision *M. fascicularis* with sweet potato, banana, peanuts, and papaya leaves (Fuentes et al., 2009). *M. fascicularis* have also been recorded opportunistically consuming invertebrates and insects (Fuentes et al., 2008). The diet of *M. fascicularis* populations in Singapore consists of anthropogenic foods, naturally occurring fruit, vegetative parts, and flowers (Sha & Hanya, 2013). Their dietary preferences have been documented to change based on different levels of anthropogenic pressure (Sha & Hanya, 2013). For example, when *M. fascicularis* groups acquire anthropogenic foods from refuse sites and through irregular provisioning, the group spends less time feeding on wild fruits and flowers and more time locomoting (Sha & Hanya, 2013). However, in other populations where they receive natural foods with regular provisioning, the groups have been documented to locomote less but also consume lower amounts of wild foods (Sha & Hanya, 2013; Fuentes & Wolfe, 2002).

Description

Macaca fascicularis are sexually dimorphic. The males weigh from 4.7 – 14 kg, whereas females weigh 2.5 – 7 kg (Gumert, 2011). *M. fascicularis* have grey/brown or brown/red fur on the dorsal side of the body and light grey/white fur on the ventral side. Their crown hair is directed dorsally. Long-tailed macaques also have significant amounts of facial hair, especially compared to other macaque species, such as *M. mulatta*. Male long-tailed macaques have cheek whiskers and hair on their upper lip that is comparable to a moustache, whereas adult females have hair on their chin that is comparable to a beard (Roonwal, 1977). Infants are born with dark brown hair, and as they grow, the fur on their body changes to lighter grey variations.

Behavior

Macaque social structure

Macaques live in multi-male, multi-female social groups that permanently contain both adult sexes as well as offspring (Balasubramaniam et al., 2018; Thierry, 2007). All macaque species are female philopatric, but there is inter-species variation in social structure, which can be observed in female social behavior (Thierry, 2008). Variation in female social behavior includes variable rates of post-conflict affiliation, affiliative contact, dominance hierarchy steepness, and asymmetry in aggression (Balasubramaniam et al., 2012; Thierry, 2008). Specifically, dominance hierarchy steepness, post-conflict affiliation, and rates of affiliative contact have been identified as phylogenetic signals within *Macaca* and create social structure covariation (Thierry, 2008; Balasubramaniam et al., 2012). To characterize interspecies social structure variation, these phylogenetic signals and other behaviors have been used to assign macaque species to a four-grade "social style" scale (Thierry, 2007; Thierry et al., 2008; Balasubramaniam et al., 2012; Balasubramaniam et al., 2018). The four-grade "social style" scale rates species from Grade 1, species with more despotic social styles, to Grade 4, species that are more tolerant or egalitarian. Grade 1 species are characterized as having steep and asymmetric dominance hierarchies and low levels of post-conflict affiliation, e.g., *M. mulatta* and *M. fuscata* (Balasubramaniam et al., 2018). Grade 4 social structures have shallow dominance hierarchies, frequent counter-aggression from subordinates, and high rates of post-conflict affiliation, e.g., *M. nigra* and *M. tonkeana* (Balasubramaniam et al., 2018). The social style of *M. fascicularis* has been ranked as Grade 2, which is referred to as mildly despotic (Balasubramaniam et al., 2018).

Within a female matriline, a female offspring's position within a hierarchy is based on the mother's rank. The mother's position in a more despotic system transfers to her daughter and determines both her lowest and highest levels of rank, meaning her lowest rank is above lower-ranked females and her highest rank sits below the mother and higher-ranked females (Chapais and Gauthier, 2004). These ranks can remain stable over an individual's lifetime and be successfully maintained through generations (van Noordwijk & van Schaik, 1999). To maintain their birth rank above other females, they create alliances, and this allows for offspring born to a high-ranking mother to out rank and maintain her dominant position even at young age against older siblings and other lower ranking adult females (Chapais and Gauthier, 2004; Young et al., 2013).

Male macaques disperse sometimes with other males, from their natal group at sexual maturity, but unlike females, may not have a stable rank over their lifetime (de Ruiter and Geffen, 1998). Males emigrate into neighboring groups and establish themselves within the male dominance hierarchy (van Noordwijk & van Schaik, 1985). Unlike females, males may fight for their dominance status, but also create coalitions, which allows them to enter new groups, overthrow dominant males, and maintain their social status (Engelhardt et al., 2004; van Noordwijk & van Schaik, 1985; Young et al., 2013). The highest-ranking male benefits from having access to reproductive females and is potentially able to father the majority of offspring during his time as the dominant male (Young et al., 2013). In some taxa, if males do not emigrate from their natal group, like females, they could inherit a dominance rank within the matriline, but if they disperse, they will physically fight for a dominant position (van Noordwijk & van Schaik, 1985) . The age of the macaque will also influence its strategy to gain a high-ranking position, for instance, older males might employ more subtle and less physically aggressive strategies to gain a high position within a hierarchy compared to younger males (Maestripieri, 2018).

Reproduction

Sexual maturity in female *M. fascicularis* is reached at approximately four years of age, and reproduction begins at five and a half years of age and sometimes later for lower ranking females (Varavudhi, Suwanprasert & Settheetham ,1992). Males reach sexual maturity between approximately four and six years of age, which is usually concurrent with emigration from their natal group (de Ruiter and Geffen, 1998; van Noordwijk & van Schaik, 1985). In captivity, sexual maturity has been recorded as early as three years of age for females, but on average four years is the most common age of parturition in captive settings (Timmerans, 1981).

Reproduction in macaques is directly linked to social rank and the group's social structure (Cowlishaw & Dunbar, 1991; van Noordwijk & van Schaik, 1985; van Schaik, Pandit, & Vogel, 2004). It is energetically costly to establish and maintain high-ranking positions, but these positions yield benefits for the female that include social, reproductive, and resource access (van Noordwijk & van Schaik, 1999). The positive effects of dominance rank are more pronounced in nepotistic societies like *M. fascicularis*. However, not all studies have yielded positive effects of dominance rank on reproductive success in similar social hierarchies, which can be attributed to three explanations: 1) the effect is only obtained under unusual ecological circumstances, in which only a few individuals can monopolize food or birth rates differ between females; 2) infant survival rates are too low to find significant differences between females, and thus, the benefits of the hierarchy cannot be clearly observed or understood; or 3) there is an insufficient amount of information to depict a group's individual relationships and social structure and therefore nullifies dominance rank as a predictor of reproductive success (Funkhouser, Mayhew, & Mulcahy, 2018; Sterck & Watts, 1997; van Noordwijk & van Schaik, 1999).

In *M. fascicularis*, females hormonally and physically signal when they are in estrus, which is a reoccurring period of sexual receptivity and fertility in female mammals, and when they are ready to reproduce (Engelhardt, Hodges, Castern, & Heistermann, 2005). Males must independently assess when a female is fertile, and there are positive correlations between male interest in females and female estrogen levels (Engelhardt et al., 2004). These increases in estrogen levels during ovulation also promote other traits that males can use as indicators for female fertility, such as female pheromone production, copulation calls, skin swellings, and behaviors (Engelhardt et al., 2004; Engelhardt et al., 2005). Sexual swellings are common in catarrhines and are correlated with the female menstrual cycle, additionally female swelling is hypothesized to be an honest signal of fertility (Dixson, 2004). In *M. fascicularis*, skin swelling is characterized by an inflation of the female's tail root and red coloration of the appending skin. Variation in swellings help identify and characterize individual females (van Noordwijk, 1985). After pregnancy and birth, the mother's reproductive cycle normalizes when their offspring reaches the approximate age of four months (Meishvili, Chalyan & Vancatova, 1991).

Mother-Infant Relationships

Macauqe mothers are usually the primary caregiver of their offspring, and their decisions are integral for the future survival of their offspring (Maestripieri, 2002; Maestripieri, 2018). There are species constraints on maternal behaviors, but within those constraints, interactions between a mother and offspring are influenced by a variety of factors, social rank influences, age, paternity, and parity, which in turn create variation between dyads (Maestripieri, 2018; van Noordwijk & van Schaik, 1999).

Parenting style

Most macaque mothers give birth to single offspring, and these offspring have a prolonged period of development, which limits the number of offspring a mother can produce within a lifetime (Blomquist, 2013). These low birth rates and long developmental periods result in a higher level of maternal investment, defined as any maternal expenditure that benefits the offspring; modes of investment include time allocation (e.g., socializing, teaching), energy output (e.g., milk production), and parenting style (e.g., rejection behaviors) (Wells, Yao, Williams, & Gayner, 2016; Pontier & Allainé, 1993). Maternal behaviors are reflective of maternal investment strategies, and in macaques, these behaviors are motivated by the dualistic nature of two maternal behaviors: protectiveness and rejection (Maestripieri, 2001). Variation in the proportion of protectiveness to rejection results in four different parenting styles: controlling, protective, rejecting, and laissez-faire (Maestripieri, 2001). A controlling parenting style is high in both protectiveness and rejection. Protective parenting is high in protectiveness and low in rejection. A rejecting parenting style is low in protectiveness and high in rejection. Finally, a laissez-faire style is low in both protectiveness and rejection (Maestripieri, 2001). Variation in maternal behavior and investment has been documented between species, between groups, and among individuals (Maestripieri, 2001). Comparisons of various macaque species have shown that differences in social organization predict differences in mothering styles, especially when it comes to tolerance of other group members and infants (Thierry, 1985). *M. fascicularis* maternal parenting style has not been as well studied as other macaque species, but due to their behavioral similarity to *M. mulatta*, *M. fascicularis* parenting style is more likely to be protective or controlling to promote infant independence by increased infant rejection (Balasubramaniam et al., 2018; Maestripieri, 1994). This parenting style in *M. mulatta* is associated with a high infant risk, which includes behaviors of harassment and rare kidnappings from other group members. These maternal styles are learned, and *M. mulatta* daughters will have a maternal style similar their mother's, particularly for rates of maternal rejection (Berman, 1990).

Social rank

Maternal rank influences an infant's health and social rank (Liu et al., 2018). In a population of *M. fuscata,* when infants faced intragroup threats, middle- and low-ranking mothers monitored their offspring more than high-ranking mothers (Nakamichi & Onishi, 2011). Due to the hierarchical social structure of some macaques' social groups, the infants of middle- and low-ranking mothers were more likely to have their infants temporarily kidnapped or handled by other high-ranking females, and thus had to intensely monitor their infants, perhaps to avoid potential threats (Nakamichi & Onishi, 2011). In *M. mulatta,* low-ranking females had longer inter-birth intervals when compared to higher-ranking females (Gomendio, 1990). Low-ranking females infants had a higher frequency of nipple contact and longer bouts of suckling, which can reproductively inhibit a mother (Gomendio, 1990). High-ranking females also tend to have resource priority and produce more milk, which then increases the fat content of maternal milk and allows infants of high-ranking mothers to reach sexual maturity earlier than lower ranking individuals in *M. mulatta* (Altmann & Alberts, 2005; Bernstein & Hinde, 2016). In contrast to these reports, studies find that dominance rank has no effect on *M. fuscata* and *M. radiata* maternal behavior (Schino, D'Amato, & Troisi, 1995; Silk, 1991). Social success in macaques is built on their matriline and hierarchical group structure. High-ranking females have more agonistic support, a greater social network, and more reproductive success, which is then passed down to their offspring who in turn rely on maternal alliances and create new alliances more easily (Maestripieri, 2018). Mothers will sometimes aid their offspring during conflicts. Higher-ranked offspring learn that lower-ranked opponents will exhibit submissive behaviors (Maestripieri, 2018), whereas lower-ranked offspring learn that their rank is adjacent to their mother's rank (Maestripieri, 2018).

Infant handling

The term infant handling is used when individuals other than the mother hold or handle the offspring (Kümmerli, 2008). In most primate species, mothers are the main infant handlers (Nicholson, 1987). The younger the infant, the more interest other females typically have in handling that infant (Silk, 1999). In *M. fascicularis,* females frequently groom mothers with infants to gain access to the infant (Gumert, 2006). Females tend to congregate to mothers with an infant more frequently than to females without infants. This behavior is common in primates (Gumert, 2006; Maestripieri, 1994; Silk, 1999). It is hypothesized that other females are attracted to infants so they can practice their maternal skills, which could lead to a higher likelihood of their own offspring's survival in the future (Silk, 1999). Sub-adult females are the age/sex class most likely to attempt to gain access to infants (Silk, 1999). Grooming is a commodity for access to infants, a female will groom a mother for attempted access to her infant (Gumert, 2006).The dominance position of female *M. fascicularis,* is stable and greatly influenced by kinship, which results in lower ranking females giving more grooming, infant handling, and tolerance of space than higher ranking females in exchange for access to infants (Gumert, 2006).

Infant age and sex

An infant's age and sex affect a mother's behavior (Maestripieri, 2018). As infants age, they become less physically dependent on their mother, and proximity to their mother decreases over time (Arroyo-Rodriguez, Serio-Silva, Alamo-Garcia, & Ordano, 2007). There is also evidence that mothers form stronger bonds with female than with male infants (Kulik, Langos, & Widdig, 2016) and provide higher amounts of maternal investment (i.e. time) to female offspring (Maestripieri, 2001). For example, *M. mulatta* mothers experience longer inter-birth intervals after a daughter is born, possibly indicating increased postnatal investment (Maestripieri, 2001). This investment is expected in a matrilineal society because young females often receive more aggression and need more protection from unrelated females (Maestripieri, 2007). Additionally, as they reach adulthood, daughters can provide social support to the mother (Maestripieri & Thierry, 2007). In *M. mulatta*, mothers are more aggressive to sons than daughters, but there is no difference in affiliative behaviors directed toward the two sexes (Kulik et al., 2016). Hinde (2013) found that mothers allocate different milk resources to different offspring. In *M. mulatta*, female offspring receive more calcium, but in first-time mothers, males receive more nutrients, such as fat, protein, and sugar (Hinde et al., 2013; Hinde, 2007). High calcium levels are thought to support early female bone calcification, and the high nutrient content for males is hypothesized to compensate for the lack of social support male offspring receive in matrilineal societies (Hinde et al., 2013; Hinde, 2007). Males with smaller body sizes are much more likely to die in juvenility and have less successful emigrations, so the mother's milk provides more nutrients to promote healthy male growth (Hinde, 2013; Hinde, 2007). As offspring grow, the mothers continue preference the female offspring, but the overall amount of investment decreases as the male and female offspring become more independent (Kulik et al., 2016). Behavioral sex differences emerge early in a macaque's life. As they mature, males spend increasingly less time with their mothers and kin than do young females, while increasing interactions with male peers (Berman, 1982). In addition, as they mature, female juveniles interact with more individuals of various ages and sexes (Bernstein & Ehardt, 1986). Maternal age influences maternal investment (Schino et al., 1995). As mothers age, they become less protective and have less ventral contact time with their offspring (Schino et al., 1995).

Group size

Group size influences mother-infant relationships. In *M. mulatta*, as group size increases, the amount of time the infant spends in close proximity to its mother also increases (Berman, Rasmussen, & Suomi, 1997). Similarly, the infant leaves the mother's proximity significantly less (Berman et al., 1997). In addition, as group size increases, the proportion of close female relatives in proximity to the infant also decreases. The mother responds with protective behavior indicative of a more controlling parenting style (Berman et al., 1997). Compared to a smaller social group during the birth season, mothers in larger groups spent less time in contact with their infant, initiate more contact and remain in closer proximity to the infant (Liu et al., 2018; Schino et al., 1995). Additionally, mothers belonging to larger matrilines exhibit higher rates of offspring rejection (Liu et al., 2018; Schino et al., 1995). In smaller *M. mulatta* groups, maternal rejection behavior is higher when infants are younger, the mothers have shorter interbirth intervals, and infant survivorship is lower (Liu et al., 2018).

Maternal behaviors

Common maternal behaviors recorded in macaques include maternal rejection, ventral contact, carriage riding, retrieval, proximity, infant on nipple, weaning, lactation, foraging, and grooming (Maestripieri, 1994; Schino et al., 1995; Silk, 1999). Ventral contact is most common in the infant stages when an infant is breast-feeding and/or sleeping on its mother (Schino et al., 1995). Proximity is a common measure of offspring independence from the mother, and it has been shown that as age increases, the distance that the infant travels from the mother also increases (Kulik et al., 2016). Infant on nipple behavior is a way to estimate time spent feeding without having to measure milk production or confirm ingestion (Berman, 1990; Bernstein & Hinde, 2016). Maternal rejection occurs when the mother prevents the infant from accessing her for ventral contact, often when the infant wants to feed or locomote on the mother (Schino et al., 1995). This behavior is indicative of the rejection mothering style and may help the offspring become more independent (Maestripieri, 2001). Additionally, grooming is an important behavior that allows other females access to both the mother and infant but is also a way for the mother and offspring to build relationships with one another and with other individuals (Gumert, 2006; Silk, 1999).

Development

Mothers shape offspring development. Mothering style influences her infant’s development, and the mother’s exhibited behaviors are critical for teaching offspring certain behaviors (Li et al., 2013). Orphans struggle to meet their developmental nutritional requirements and have a high probability of becoming ill and malnourished without breast milk (Hinde et al., 2013; Tardif, Power, Oftedal, Power, & Layne, 2001). Alloprimates without a biological mother have a higher rate of mortality and exhibit social developmental handicaps, including high rates of stereotypic behaviors, self-harm, and personality changes (Blomquist, 2013; Latham, 2008; von Borell, 2000; Kulik et al., 2016). In macaques, mothers shape their offspring's social future, and offspring relationships frequently mirror the mother's (Maestripieri, 2018). Mothers also contribute to their offspring's social success, and without a social network, offspring with absent mothers struggle to adapt, create alliances (Maestripieri, 2018), and may be susceptible to aggression from other individuals (e.g., infanticide). Without learning opportunities from the mother, offspring are also likely to struggle cognitively. For example, in chimpanzees (*Pan troglodytes*), mothers show their offspring how to use tools to forage for food sources (Visalberghi & Fragaszy, 1990), and *M. fascicularis* mothers are known to over-exaggerate tool use to enable their offspring to socially learn (Masataka, Koda, Urasopon, & Watanabe, 2009). This social learning dynamic is critical for the offspring's locomotive, mental, and nutritional development (Maestripieri, 2018).

Endangerment status and human conflict

According to the IUCN Red List, *M. fascicularis* is rated as a species of least concern in terms of extinction, although the population trend is decreasing (Ong & Richardson, 2008). Their population decrease is due to conflict with humans, both in terms of depleted land space and because of human exploitation for biomedical research (Ong & Richardson, 2008; Nijman & Healy, 2016). The population size of *M. fascicularis* is not well documented, although the earliest estimates were approximately 3,726,860 (Mackinnon, 1986) or 5,000,000 individuals (Fooden, 1995). Only 11 years later, Fooden predicted a 40% population decline, with an estimate of 3,000,000 long-tailed macaques still present (Fooden, 2006).

Asian primate taxa have been traded in the greatest quantities globally (Nijman & Healy, 2016) with *M. fascicularis* representing 86% of all primates in the captive-bred trade and 53% of primates exported from the wild (Nijman & Healy, 2016, p.138). They are followed by *M. mulatta* (7% of the captive trade and 4% of the wild trade) and *Chlorocebus* spp. (<1% of the captive trade and 14% of the wild caught trade) (Nijman & Healy 2016, p.138). Because *M. fascicularis* are heavily exported, breeding populations have been made for the purposes of human harvesting (Kyes et al., 1998). The top importers of captive bred *M. fascicularis* are the United States, Japan, China, France, and the United Kingdom (Nijman & Healy, 2016). These monkeys are used for medical product testing, surgical technique practice, social experiments, and other general risk assessments or benefits to humans (Luft, Sternberg, Fine, & Sarazan, 2013; Niggeman, Niehoff, Sternberg, & Weinbauer, 2011; Smith, Devito, & Harlow, 1959; Nijman & Healy, 2016).

M. fascicularis populations also experience high amounts of human conflict. As humans expand their agricultural practices and contribute to deforestation, more alloprimate-human conflict arises (Campbell-Smith et al., 2010; Fuentes et al., 2005). However, *M. fascicularis* is considered holy in many cultural communities throughout southeast Asia, and their populations are frequently provisioned (Ilham, Rizaldi, Nurdin, & Tsuji, 2017; Fuentes, 2010; Fuentes et al., 2007). Because of some primates’ ecological flexibility (and pushed by human encroachment), many species have moved into urban areas where they live by using human resources and human waste as food resources (Ilham et al., 2017). This alloprimate-human dynamic creates a conflicting view of *M. fascicularis* as not only a holy relic, but also a pest and even an invasive species (Ilham et al., 2017; Fuentes et al., 2005).

Anthropogenic effects can also influence macaque behavior depending on location and species (Fuentes et al., 2008; Sha & Hanya, 2013). *M. fascicularis* groups that have higher anthropogenic contact rates spend less time resting and more time locomoting (Sha & Hanya, 2013). By contrast, resting and grooming in *M. mulatta* is significantly higher in urban macaques compared to those experiencing less anthropogenic activity (Jaman & Huffman, 2013). Similar activity budget differences have been observed in *Chlorocebus aethiops*, those that had higher human food consumption spent a larger portion of their activity budget resting and lower amount of time feeding (Saj et al., 1999). Even vocalization behaviors are affected by anthropogenic factors; for example, *Alouatta palliata* in the interior of a fragmented forest howled longer than those on the edge (Bolt et al., 2019). Anthropogenic disturbance coupled with close human-alloprimate genetic relatedness, has resulted in the high rates of pathogen exchange (Gillespie, Nunn, & Leendertz, 2008). In a continually changing world, zoonoses of retroviruses (i.e. simian foamy virus), filoviruses (i.e. ebola virus), bacterial, fungal, and parasitic pathogens will become even more transmissible between alloprimates, humans, and domesticated animals (Gillespie et al., 2008).

Parasites

Parasites are eukaryotic or prokaryotic organisms that live a substantial portion of their lives in (endoparasite) or on (ectoparasite) a different kind of organism (the host), usually with a nutritional dependence on said host (Jacobs, Fox, Gibbons, & Hermosilla ,2015; Taylor et al., 2016). To be considered parasites, they must be attached to one host in its life cycle, if not more (Taylor et al., 2016). An obligate parasite is one that is entirely dependent on its host, and a facultative parasite is an independent organism that can complete its life cycle without the host

(Taylor et al., 2006). Parasites that exploit multiple hosts have complex life cycles (Taylor et al., 2006). The parasite's stage of life and function relative to the host determines the host terminology. There are several ways that hosts are defined by these parameters. A final, definitive, or primary host is one in which sexual reproduction of the parasite occurs (Jacobs et al., 2015; Taylor et al., 2016). An intermediate host is one in which the parasite develops during its intermediate life stages or when asexual reproduction occurs. A transport or paratenic host is one that the parasite takes advantage of only as a vehicle, usually has a more passive effect, and is not there for a large portion of its life (Jacobs et al., 2015; Taylor et al., 2016). A reservoir host is a host population that the parasite lives in to infect other organisms (Jacobs et al., 2015). The effects of parasites on the host are complicated, and parasites themselves are extremely adaptable to the host's immune response to their invasion (Whitfield, 1993). Some parasites cause minimal damage to or mild discomfort for their hosts, whereas others carry serious diseases, impair their host's immune function, amplify other impairments of the host, and even cause mortality (Friant, Ziegler, & Goldberg, 2016; Hisler, Smith, & Smith, 2014; Ulrich et al., 2010; Whitfield, 1993).

Helminths consist of three major groups of parasitic worms that include nematodes (roundworms), trematodes (flukes), cestodes (tapeworms), and one minor group, the Acanthocephala (thorny-headed worms) (Jacobs et al., 2015; Taylor et al., 2016; Whitfield, 1993). There is an estimated 75,000 to 300,000 different parasitic species of extant helminths in vertebrates (Jacobs et al., 2015; Taylor et al., 2016; Whitfield, 1993). Trematodes (flukes) are separated into two main subclasses: the Monogenea, who have direct life cycles, and the Digenea, who require intermediate hosts to survive (Taylor et al., 2016). The digenetic trematodes are mostly found in the bile duct, the digestive tract, and the vascular system. Digenetic trematodes are exclusively found in vertebrates and are more common than monogenetic trematodes. Every species of cestode is parasitic and is notably different from other classes of parasitic worms based on its unique morphological characteristics and highly specialized life cycles. Acanthocephalans, the thorny-headed worms, are obligatory endoparasites of vertebrates (Wernery, 2016). Non-helminth species, such as Protozoans are frequently found parasites across vertebrate taxa. There are currently 13 recognized protozoan phyla, and approximately nine taxa are considered parasitic.

Morphology

In the phylum Nematoda, there are two classes and six orders, and there is morphological variation within and between orders. In general, nematodes are cylindrical in shape, have an unsegmented body that tapers at each end, are bilaterally symmetrical, and covered by a colorless, relatively translucent, tough, outer layer referred to as the cuticle, which is covered with small longitudinal ridges (Taylor et al., 2016). Their body remains in a cylindrical shape due to their hydrostatic skeleton or tube-like inner structures that suspend freely within their body cavity. The underlying hypodermis secretes the cuticle and carries two lateral cords, one of which carries the excretory canal and the other carries the nerves that run longitudinally within the body. Their muscles are situated below the hypodermis but above the body cavity. The muscles contract while alternating from dorsal to ventral sides thus allowing the parasite to locomote. The digestive tract starts with an opening at one end of the body for the mouth (stoma) and is equipped with two or three lips that lead to the esophagus. Some nematode mouths open into a buccal capsule, which contains blades or teeth. If a nematode has a buccal capsule, they use it feed on mucus from their host. The esophagus is muscular and pumps food from the mouth to the intestine (Taylor et al., 2016). There are several morphological variations in nematode esophagi: filariform, which is simple and slightly wider posteriorly; bulb-shaped with obvious large posterior swelling; double bulb-shaped with two posterior swellings stacked on top of one another; muscular-glandular, which has a muscular anterior but a glandular posterior; trichuroid, in which the esophagus is a thin single line of capillaries; and rhabditiform, which has slight posterior and anterior swellings. The intestine then follows the esophagus, which is a simple non-muscular tube of lumen enclosed by cells. The intestine differs between male and females nematodes. In females, the intestine connects to the rectum and ends in the anus, where as male intestines end in the cloaca. Most nematodes are dioecious, and the sexes have different reproductive organs. The organs are filamentous tubes and float in the body cavity. Males have tubular testes that connect to the seminal vesicle, which ducts sperm to the cloaca. All females have an ovary oviduct, and a uterus that can be paired or single and ends at the vagina that opens at the vulva. Female organ placement and order can help determine the species of helminth (Taylor et al., 2016).

Adult trematodes are leaf-shaped, their bodies are tegumentary, covered in spines/scales, and have two muscular suckers that allow the parasite to eat and attach itself to the host. Flukes have a single oral opening that leads to the pharynx, then the esophagus, a pair of caeca that have no output, and no anus. This means that material that is undigested is regurgitated. The material that is digested is excreted from ciliated flame cells, which are a series of tubules that open to the worms exterior and regulate osmostic pressure. The nervous system consists of two longitudinal trunks that connect anteriorly with ganglia. The male organs consist of a pair of testes that lead into a vas deferens, which join the seminal vesicle and cirrus. Females have a single ovary that is attached to an oviduct, which expands into the ootype. The ootype produces a yolk that hardens to give the egg a protective shell, which is eventually expelled through the genital pore next to the oral sucker (Taylor et al., 2016).

Cestode bodies have no body cavity and are tape-like in shape. The tegument of the body is absorptive and below it lies the muscle and syncytium cells. The nervous system consists of ganglia in the scolex that runs posteriorly. Tapeworms found in alloprimates usually have spherical heads or a scolex-bearing organ (with four suckers and hooks), which is attached to an unsegmented neck and a segmented body (one segment is a proglottid, multiple segments are a strobila). Proglottids continually grow from the neck, and each can contain one or two sets of reproductive organs and is considered hermaphroditic. Genital pores open from each proglottid allowing both self- and cross-fertilization. As the tapeworm grows, the internal structure of its body dissipates, which allows the worm to shed its segments filled with organs containing fertilized eggs (Taylor et al., 2016).

Acanthocephalans morphology is variable, but all species have a unique and specialized fixatory organ, referred to as the proboscis, that is armed with spines (Wernery, 2016). The spines attached to the proboscis can be variable in shape, from long and slender, to short and sturdy. The proboscis itself is hollow, and is separated from the body cavity by a proboscis sheath, but is attached the body cavity by muscle-strands. The worm uses its proboscis to insert itself into the hosts intestinal wall. Acanthocephalans do not have a mouth and instead, take in nutrients through their body surface. The adults vary in size, from several millimeters to over 10 cm (Castro, 1996). They are diecious and have subtle sexual dimorphism differences (Wernery et al., 2016).

Protozoa are eukaryotic organisms and contain a nucleus, endoplasmic reticulum, mitochondria, a Golgi body, and lysosomes. Protozoa can have a free flagellum, a single, or even multiple flagella, which allows the organism to locomote. In some species, the cell membrane contracts when the flagellum beats, which undulates the membrane and enhances motility. Some Protozoa have cilia instead of flagella, which are fine hair-like organelles, identical in structure to flagella, that cover the exterior surface and beat in unison for locomotion and occasionally move food toward itself. Some Protozoa also locomote with pseudopodia, which are extensions of cytoplasm that can also be used to cup and consume food material. Food material is processed through lysosome fusion or the cytosome, and the undigested portion is excreted from the cell. (Taylor et al., 2016).

Life cycle

After hatching, a nematode has five life stages designated L_1, L_2, L_3, L_4, and L_5. Newly hatched nematodes (L_1) grow by feeding on bacteria until molting (See Figure C1 for a generalized life cycle of intestinal nematodes). Molting occurs by the synthesis of a new cuticle and exsheathment, where the old cuticle is loosened, and the larva ruptures the cuticle and escapes. The nematode is considered pre-parasitic from egg until mid-way in the L_3 stage of development, after which they become parasitic. For the nematode to successfully be parasitic in this stage they must be in their definitive or final host, whereas the pre-parasitic phase occurs when the nematode is in the external environment or still residing in its intermediate host. Nematodes have both direct and indirect life cycles and these dictate how the parasite develops. Direct life cycles are when all the pre-parasitic stages of the organism occur in a free-living environment and their development takes place inside the egg or after hatching (Johnstone, 1998). In some species, the egg, L_1, and L_2 stages takes place in the environment, after which the juvenile is ingested (L_3), and migration through the definitive host occurs (L_4) until the parasite reaches its final site, where it becomes an adult and lays its eggs (Taylor et al., 2016). L_5 represents the end of immaturity and the entrance into the adult stage of life, during which they become sexually mature (Fig. 1). Indirect life cycles are where the larvae develop in an intermediate host before moving on to its definitive host (Johnstone, 1998). The egg is excreted and then picked up for the L_1 and L_2 life stages in an intermediate host, the L_3 stage occurs during ingestion by the definitive host, and migration through the definitive host occurs (L_4) until the parasite reaches its final site, where it becomes an adult and lays its eggs (Taylot et al., 2016). There is some variation to this life cycle in different nematode genera, but all follow the same basic life cycle pattern of egg, L_1-L_5, adult, and then the production of new eggs. The transmission of nematodes usually occurs through the ingestion of an egg or larvae, when the intermediate host is eaten by the final host, or skin penetration, e.g., a mosquito bite.

The life cycle of trematodes is complex and variable. All trematodes start as an egg, usually laid within the intestine of a host. The egg is then expelled by the host and ends up in a water source. Here the egg hatches into a larva known as a miracidium and usually searches for an aquatic intermediate host, e.g., a mollusk. The miracidium locomotes with small cilia through the water and does not feed until it finds a new host (Taylor et al., 2016). Within the intermediate host the miracidium loses its cilia and develops into a redia or sporocyst, which has some adult morphology such as a mouth, gut, and appendages for locomotion. The larva continues to develop into the cercaria and searches for a secondary intermediate host. In trematodes, such as Schistosomes, the cercaria becomes a metacercaria with its secondary intermediate host, which can be not only a vertebrate but also vegetation. During this stage, the organism becomes infective and travels through its definitive host through ingestion of another organism eating its secondary intermediate host. Finally, in the definitive host, it develops into an adult and reproduces. The spread and reproduction of trematodes can happen swiftly in its intermediate host due to their asexual reproduction known as parthenogony.

Cestodes reside in the small intestines of their final hosts. Species life cycles are specialized and frequently involve transferring to specific intermediate hosts, except for in *Hymenolepis nana*, which has a one host life cycle and is spread via direct transmission (Heyneman, 1996). The general life cycle consists of eggs being laid by an adult, excreted from the parent's final host, and is picked up by an intermediate host. Generally, cestodes lay a huge amount of eggs within its host. For instance, *Taenia saginata* (beef tapeworm) lays 50,000-100,000 eggs within its intermediate bovine host (Heyneman, 1996). In the intermediate host, it hatches from the activation of various intestinal enzymes and uses its hooks to tear into the blood stream or body cavity. The larva can develop into a variety of different forms (metacestodes), such as a cysticerus, coenurus, strobilocercus, hydatid, cysticercoid, and tetrathyridium. Most of the variations consist of a cyst-like structure with a scolex attached. The intermediate host expels them and a final host eats the intermediate host and ingests the metacestode. The scolex attaches to the mucosa of the host and its cyst-like structure becomes detached from its body and is digested. This is when the proglottid segments begin to grow from the base of the scolex and the metacestode develops into the full adult form (Taylor et al., 2016).

Acanthocephala have an indirect life cycle. Eggs embedded with the larval stage (acanthor) are secreted through the hosts feces and are then acquired by the intermediate host, usually a crustacean or insect (Wernery et al., 2016). Once in the intermediate host the acanthor leaves the egg and migrates from the gut to the body cavity where it forms a second larval stage known as the acanthella (Wernery et al., 2016. In the body cavity the acanthella transforms into the infective cystacanth stage. When the first intermediate host is ingested, the cystacanth is released and if the new host is suitable, the cystacanth will develop into an adult and use the new organism as its definitive host (Wernery et al., 2016). If not suitable, the organism will serve as a paratenic host, and wait until it is consumed by the definitive host. In the definitive host, the worm will attach itself to the hosts intestinal wall with its proboscis, where it will develop sexual organs, and eventually mate (Castr, 1996).

Both sexual and asexual reproduction is found within protozoans and some alternate between sexual and asexual reproduction in their life cycles. The organism will asexually reproduce by schizogony, where multiple mitoses form numerous daughter cells, but eventually undergo sexual reproduction of gametogony to produce gametes. The gametes then asexually reproduce producing sporozites that infect new hosts. Protozoa also reproduce through binary fission where the organism duplicates its organelles and cytokinesis occurs (the division of the cell at the end of mitosis or meiosis (Taylor et al., 2016).

Pathogenesis

The most common pathology from helminths is damage resulting from the blockage of internal organs from the pressure applied by developing parasites (Wakelin & Walliker, 1996). Other common pathology is damage to the mucosa which can cause physical and chemical damage to the hosts tissue (Wakelin, 1996). Many species of helminths migrate through a host’s body to complete at least a portion of their life cycle. Migrations can cause damage to tissue directly, as parasites will break through tissue to reach certain areas of the body, and cause hypersensitivity reactions (Wakelin, 1996). The most common organs that are damaged through migrations are the skin, lungs, liver, and intestines and petechial hemorrhages, skin reactions, eosinophilia, and granulomatous lesions can occur signs of parasitic infection (Wakelin, 1996).

Notably, feeding by worms upon host tissue can induce hyperplastic and metaplastic changes in tissues (Wakelin, 1996).

Nematodes

Clinical infection of *Trichuris* is usually asymptomatic. Severe infections have resulted in hemorrhagic colitis and proctitis. Fatal cases of whipworm infections have been documented in many alloprimate species including baboons, colobines, captive chimpanzees, and conocolor gibbons. Trichuris infections have also been documented to effect free-ranging red colobus temporal patterns and activity budgets (Modry, Pafčo, Petrželková, & Hasegawa, 2018).

Strongyloides are commonly found nematodes in vertebrate taxa across the world. Infections are usually asymptomatic. In humans, symptoms of *Strongyloides* infections consist of abdominal pain, diarrhea, Löffler's syndrome, which occurs during migration of filariforme larvae, and urticarial rashes. In immunocompromised humans can develop serious diseases that result in death due to larval migrants invading certain organs. Diarrhea and hyper infection has been documented in multiple alloprimate species including orangutans, gibbons, and other captive alloprimates (Modry et al., 2018).

Ascaris clinical impact is quite low since the majority of infections are asymptomatic. High numbers of *Ascaris* worms, that migrate through the liver, bile duct, and bowels, can create blockages that have caused death in large bodied apes (Modry et al., 2018).

Mammomonugamus prevalence is relatively low across alloprimate studies (Modry et al., 2018). Their pathogenicity commonly consists of mucosal inflammation and damage to the respiratory tract, because the adults attach themselves to the mucosa and mechanically block the tract. In Orangutans, *Mammomonogamus* infections are thought to have attributed to the death of five semi-captive individuals. The Orangutans exhibited symptoms of listlessness and dyspnea, and their subsequent necropsies showed *Mammomonogamus* worms throughout the individuals' respiratory tracts (Modry et al., 2018). Other Orangutans at the rehabilitation also showed symptoms of coughing, and tested positive for *Mommomonogamus* infection (Modry et al., 2018).

Anclyostoma is commonly found in free ranging alloprimates (Modry et al., 2018). In humans, *Anclyostoma* infections have caused both anemia and protein-deficiency. This is due to the hematophagous adult hookworm attaching itself to the intestinal mucosa of its host, which results in host blood loss (Modry et al., 2018). Laboratory chimpanzees also developed anemia when infected with *Anclyostoma* and orangutans in rehabilitation settings that were infected with *Anclyostoma* suffered severe physical decline (Rijsken, 1978; Orihel, 1971).

Enterobius worms have been detected in both captive and free-ranging wild alloprimates. The clinical impact of *Enterobius* is predicted to be low in wild populations and is most likely asymptomatic. However, serious symptoms have occurred in captive individuals who are heavily infected, including anal or vaginal pruritus, abdominal pain, constipation, diarrhea, vomiting, and anorexia. *Enterobius* is suspected to have caused the death of one or more captive chimpanzees (Modry et al., 2018).

Trematodes

Trematode pathogenic symptoms are mainly seen in the adult life stages. Limited literature exists for pathogenic effects in alloprimates, but orangutans inflicted with *G. hominis* were said to suffer from enteritis. *Schistosomes* are a highly prevalent and common trematodes acquired mainly through water sources, and they can cause serious pathological effects.

Schistosoma infections are frequently fatal in humans and the effects seen in humans were almost identical to those seen in captive chimpanzees. The chimpanzees exhibited symptoms of loss of appetite, muscular wasting, lethargy, jaundice, and diarrhea. Different species of *Schistomes* create vastly different pathologies. *Schistosoma haematobium* mainly effects the bladder and can cause ulcerations, hyperplasia, necrosis, obstruction, and calcification of the bladder mucosa. *S. haemotobium* can also result in damage to the liver, colon, appendix, rectal mucosa, and lungs. No urogenital damage was found in captive gibbons and chimpanzees infected with *S. haemotobium.S. japonicum* and *S. mansoni* can cause damage to the liver, lungs, and intestines. Most trematodes are generally not considered to be a serious pathogen (Modry et al., 2018).

Cestodes

Cestode adult worms can cause allergic reactions in humans, causing symptoms of headache, dizziness, inanition. More severe effects can be seen in several species of cestode, this includes physical damage to the intestines, erosive action and inflammation by scolex hooks, and reduced vitamin B12 levels. Additionally, little or no pathology can be found in certain species with light infections (Heyenman, 1996).

Acantocephala

Acantocephala infections are usually asymptomatic, but can cause gastrointestinal distress with symptoms of diarrhea, abdominal pain, anorexia, weight loss, vomiting, and constipation. Reported infections in alloprimates are usually not associated with the listed symptoms. Obstruction of the intestines from Anantocephala worms have been seen in necropsied mountain gorillas (Modry et al., 2018).

Protozoa

Balantoides, especially *B. coli*, is a commonly found ciliate within captive and free-ranging alloprimates. *Balantoides* infections are mostly asymptomatic, but serious infections have occurred and caused mortality in captive large-bodied apes (Lankester et al., 2008). Symptoms include mild diarrhea or even fulminating dysentery.

Two *Entamoeaba* species have serious pathological effects. *E. histolytica* and *E. nuttallii* can cause hemorrhagic dysentery, liver abscesses, and other intestinal pathologies. Both species of Entamoeba have been identified in both captive and free-ranging alloprimates. Additionally, *E. coli, E. hartmanni, E. dispar,* and *E. invadens* have been identified within alloprimates.

Chilomastix infections effect both humans and alloprimates and have been reported to be mostly asymptomatic. Though *Chilomastix* has been identified in alloprimates, an understanding on their pathogenic impact has not be explored.

Modes of parasite transmission and acquisition

Parasites are transmitted and acquired in a variety of ways. Exposure to parasitic infections are mainly influenced by climate, hygiene, food preferences, and contact with vectors (Castro, 1996). Common transmission strategies include close sexual contact, close non-sexual contact, close contact via vertical transmission, distant and/or environmental contact, vector-borne, or complex life cycles with intermediate hosts (Nunn & Altizer, 2006). Close contact non-sexual behaviors commonly include biting, scratching, grooming, touching, and huddling increases parasite transmission, such as ectoparasites and parasites that spread via fecal-oral transmission (Nunn & Altizer, 2006). Vertical transmission occurs via parent-offspring interactions and parasites are commonly passed through the mother's milk. Vertical transmission is observed with *Toxoplasma gondii, Trypanosoma cruzi,* and *Anclyostoma duodenale* (Nunn & Altizer, 2006). Non-direct and/or environmental transmission is one of the most common parasite transmission methods. Individuals contract parasites from fomites, contaminated soil, water, food, or from free-living parasites within their habitat. This includes *Isospora spp*., *Strongyloides spp.,* and *Paragonimus westermani*, which are transmitted through the environment (Nunn & Altizer, 2006). Vector-borne parasite transmission is caused by biting arthropod vectors, resulting in *Trypanosoma, Plasmodium,* and yellow fever (Nunn & Altizer, 2006). Lastly, some parasites have complex life cycles and only survive by being transferred to a new host, usually through the ingestion of the intermediate host or contact during the infective stages (Nunn & Altizer, 2006). Parasites such as *Taenia, Schistosoma, Filariopsis,* and *Mansonella* are transmitted through digestion of the intermediate host or direct contact during the infective stages (Nunn & Altizer, 2006). Acquisition is the receiving end of the transmission cycle. Alloprimates commonly acquire parasitic infections from contact with other individuals, fecal contamination, their natural environment, or eating infected food sources or organisms that carry a parasite themselves (e.g., insects or fish) (Nunn & Altizer, 2006).

Age

Species with longer lifespans, such as alloprimates, should encounter more parasites than those with shorter lifespans (Nunn & Altizer, 2006). Individual immune defenses are weakest at the start and end of life (Lloyd, 1995) and are related to epidemiological and immunological processes (Nunn & Altizer, 2006). Young individuals are disproportionately affected by parasites in humans (LeBraud et al., 2015; Hall et al., 2008), and this is supported by the alloprimate literature. For example, young olive baboons (*Papio anubis*) carry greater endo- and ectoparasite loads than other age classes (Eley, Strum, Muchemi, & Reid, 1989). At Gombe National Park, young *P. anubis* individuals had a higher prevalence of *Strongyloides* and *Schistosoma mansoni* (Müller-Graf, Collins, & Woolhouse, 1996; Müller-Graf, Collins, Packer, & Woolhouse, 1997). Infant vervet (*Cercopithecus aethiops*) and yellow baboons (*Papio cynocephalus*) had the highest infection rates of *Strongyloides* (Meade, 1984). It was suggested that the infant's acquisition of *Strongyloides* was influenced by vertical transmission, which later allows the individual to develop partial immunity (Meade, 1984).

Parasite modification of host behavior

Behavioral modification of a host by a parasite is common and occurs to increase the fitness of the parasite (Soghigian, Valsdottir, & Livdahl, 2017). *Yersinia pestis* infects fleas, a vector for the bacteria, and forms a mass in the flea's protoventriculus (Loker & Hofkin, 2015). The bacteria create a blockage and the flea can no longer feed, which causes the flea to attempt to feed more often, thus allowing the bacteria to spread to its definitive host (Loker & Hofkin, 2015). *Toxoplasma gondii* manipulates their intermediate host, the rat, so they become more susceptible to being eaten by the definitive host, the cat (Vyas, Kim, Giacomini, Boothroyd, & Sapolsky, 2007). In Vyas et al. (2007), rats were injected with *T. gondii* and placed in an enclosure with four different environments: unscented, scented with bobcat urine, scented with rabbit urine, and the area where the rat nested. Uninfected rats spent 35% of their time in the quadrant scented with bobcat urine, and infected rats spent 60% of their time in the quadrant scented with bobcat urine (Vyas, Kim, Giacomini, Boothroyd, & Sapolsky, 2007). *T. gondii* is hypothesized to also effect human behavior (Flegr, 2007). Personality and locomotor differences were observed between uninfected and infected or previously uninfected individuals (Flegr, 2007). Infected men exhibited lower rule consciousness and higher vigilance, thus were more likely to disregard rules and exhibit more reckless behaviors. By contrast, infected women exhibited higher warmth and higher superego strengths, exhibiting more moralistic and conscientious behaviors (Flegr, 2007). Additionally, subjects were given computerized motor skill tests, and those infected with *T. gondii* performed poorly and lost their concentration more frequently, suggesting that *T. gondii* could impair motor performance in humans (Flegr, 2007).

Parasite behavioral modification has not been widely explored within alloprimates, but human behavioral differences suggests that parasites could also affect alloprimates. Alloprimates are intermediate and definitive hosts to many species of parasites (Nunn & Altizer, 2006). For instance, *Echinococcus* spp. have been suggested to increase predation on intermediate hosts by creating chest pain symptoms, thus limiting the host's response during a predator attack (Moore, 2002). *Toxoplasma gondii* has shown to effect fear behavior in lab rats and captive chimpanzees (*Pan troglodytes troglodytes*), as well as human personality (Poirotte et al., 2016; Vyas et al., 2007). In comparison to uninfected chimpanzees who showed aversion to *Panthera pardus* (a natural predator) urine, chimpanzees that were infected with *Toxoplasma gondii*, lost their aversion towards the urine of *Panthera pardus* (Poirotte et al., 2016). *Toxoplasma gondii* has been identified in both baboons and howler monkeys (McConnell et al., 1974; Stuart et al., 1998). It has been postulated that since parasites manipulate their intermediate host to increase transmission to their definitive host in humans, such as tsetse fly vectors of trypanosomes, that this relationship could also affect alloprimates (Nunn & Altizer, 2006).

Non-human parasitic studies

Parasites can cause minimal damage to their host or in extreme cases mortality (Friant, 2016; Hisler, 2014; Ulrich, 2010; Whitfield, 1993). A study on the European shag (*Phalacrocorax aristotelis*) has shown that based on an offspring's standing in the hierarchy, parasites have different consequences for different offspring (Reed et al., 2012). This includes the youngest hatchling growing significantly slower in a parasite-ridden nest but faster than its siblings in a parasite-free nest (Reed et al., 2012). In dogs, helminths, such as the dog roundworm (*Toxocara canis*), a common dog hookworm (*Ancylostoma caninum*), the double-pored dog tapeworm (*Dipylidium caninum*), and a genus of tapeworms (*Echinococcus*), affect canine health and cause morbidity and mortality (Moskvina & Ermolenko, 2016).

Alloprimate parasite studies

Common alloprimate gastrointestinal parasites include *Strongyloides* spp., *Trichostrongylus* spp., *Oesophagostomum* spp., *Enterobius* spp., and *Ascaris* spp. Previous research on helminth effects in alloprimates has mainly focused on how habitat fragmentation affects the host-parasite relationship, as well as the acquisition and transmission of parasites (Gillespie & Chapman, 2008; Hussain et al., 2013; Klaus et al., 2017; Tiwari, Reddy, Predheeps, Sreenivasamurthy, & Umpathy, 2017). Studies have shown that parasite dynamics can correspond with host population size in a fragmented forest, and that parasite prevalence and richness is directly related to habitat fragmentation, especially those with high anthropogenic activity (Gillespie & Chapman, 2008; Hussain et al., 2013; Klaus et al., 2017; Tiwari et al., 2017). However, the effects of these parasites on the behavior of the alloprimates in these studies remain relatively unexplored. Overall, nematodes were the most common helminth group observed (Hussain et al., 2013; Kvapil et al., 2017; Klaus et al., 2017; Li, Ren, Li, Zhu, & Li, 2017; Tiwari et al., 2017). Regularly, other groups of helminths and protozoa, including cestodes, trematodes, and various protozoa, were found but usually in less abundance (Corréa, Bueno, Soares, Vierira, & Muniz-Pereira, 2016; Hussain et al., 2013; Kvapil et al., 2017; Klaus et al., 2017; Li et al., 2017; Tiwari et al., 2017).

In southeast Asia, many humans keep alloprimates as pets, including *M. fascicularis* (Jones-Engel et al., 2004). Zoonotic disease transmission becomes extremely likely with frequent close contact with humans. In a parasite study of eight species of pet macaques in Indonesia, seven taxa of protozoa and two taxa of nematodes were detected (Jones-Engel et al., 2004), including *Blastocystis hominis, Iodamoeba bütschlii, Entamoeba coli, Entamoeba hartmanni, Chilomastix mesnili, Endolimax nana, Retortamonas intestinalis,* hookworm, *Trichuris* spp., and *Ascaris* spp. (Jones-Engel et al., 2004). In another case study of 117 alloprimate species (36 threatened and 81 non-threatened), threatened species had lower parasite richness and diversity compared to non-threatened species (Altizer, Nunn, & Lindenfors, 2007). In Taï National Park, 23 gastrointestinal parasites were identified in seven cercopithecines (Kouassi et al., 2015). In total, nine protozoa, 13 nematodes, and one trematode were identified from this assessment (Kouassi et al., 2015). In a comparative study of vervet monkeys, those that lived in urban environments had higher parasite richness and abundance than those that lived in semi-urban and primate reserve environments (Thatcher, Downs, & Koyama, 2018). *Trichuris trichuria* and *Strongyloides* spp. are the most two prevalent parasites observed in Nilgiri langurs (*Trachypithecus johnii*), which reside in fragmented landscapes in India. In this study, anthropogenic effects, such as human proximity and tree cover, had no effect on parasite loads

(Tiwari et al., 2017). In *Presbytis rubicunda*, seven helminth and four protozoa taxa were recovered from the feces of an adult female who became ill and eventually died. This increased parasite prevalence indicates that parasite overload can cause death in *Presbytis rubicunda* (Hilser et al., 2014).

In general, macaques are host to multiple parasite taxa. In lion-tailed macaques (*M. silenus*), high anthropogenic pressures that promote zoonotic disease increase gastrointestinal parasites (Hussain et al., 2013). In *M. fuscata*, parasite transmission is based on social network placement, i.e., directly transmitted parasites (nematodes) in females increases with dominance rank (MacIntosh et al., 2012). In a survey of 20 bonnet macaque (*M. radiata*) groups, 19 of the groups had endoparasites (Kumar et al., 2018) and 21 taxa were recorded, including 16 helminths and five protozoans (Kumar et al., 2018). The increase in parasites in this population helps explain why immature survival and birth rate is low in fragmented forests in India (Hussain et al., 2013). Highly pathogenic and zoonotic parasites, including *Giardia* sp., *Entamoeba* sp., and *Entamoeba coli*, have been identified in *M. mulatta* living within both urban and semi-rural environments in India (Debenham, Tysnes, Khunger, & Robertson, 2017). Parasites have been reported in *M. fascicularis* in both captive and natural settings. Breeding facilities in China report a high protozoan prevalence (87.40%) and low helminth egg prevalence (2.03%) (Zanzani, Gazzonis, Epis, & Manfredi, 2015). In an anthropogenic mangrove forest in Ho Chi Minh City, *Oesophagostomum* sp., *Anclyostoma duodenale, Trichostrongylus*, and *Trichuris trichura* were identified (Son, 2002). In Bali, environmental and anthropogenic landscape components were tested to understand how they affected the prevalence, intensity, and diversity of parasites in *M. fascicularis* (Lane, Holley, Hollocher, & Fuentes, 2011). In total, 18 species of parasites were identified across multiple temple sites (Lane et al., 2011). It was found that nonanthropogenically driven landscapes have no effect on parasite prevalence, but anthropogenically transformed landscapes can alter the prevalence of parasites in *M. fascicularis* (Lane et al., 2011).

Body Condition

Body condition is an important health indicator and is a subjective method of assessing body fat and muscle (Burkholder, 2000). Specifically, a body condition scale can be useful in understanding individual variation of nutritional adequacy, resource use, reproductive condition, pathogen presence, and even social ecology (Millette, Sauther, & Cuozzo, 2015; Ichino et al., 2013; Clingerman & Summers, 2005; Reynolds & Braithwaite, 2001; Coleman, 1993). In previous studies1 (Borg, Majolo, Qarro, & Semple 2014; Fuentes, Shaw, & Cortes, 2007). A veterinary assessment is the most common way to evaluate body condition (Millette et al., 2015; Clingerman & Summers, 2005). A body condition chart has been established for *M. mulatta*, but for a laboratory setting, which involves scale measurements and physical palpitation (Clingerman & Summers, 2005). Although this is effective for laboratory alloprimates in a controlled setting, a visual scoring system would allow for a simpler and non-invasive measure. Furthermore, a body condition chart for free-ranging macaques is more translatable to the field and useful for future conservation practices (Milette et al., 2015; Reynolds and Braithwaite, 2001). However, a body condition chart has not been created for long-tailed macaques, one of the most widely distributed and common alloprimate species found in anthropogenic landscapes (Sha, 2013; Fuentes et al., 2007).

Table 1

Body Condition Chart

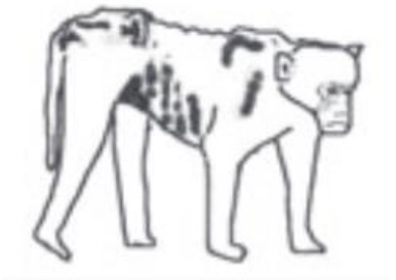
Body Condition Chart				
Score	Descriptor	Description	Photo	Sketch (Clingerman & Summers, 2005)
1	Emaciated	**Body shape:** Very angular, rigid body outline, below average body mass scapula, and ribs. **Morphology:** Underlying skeletal structure very visible. Very prominent hip bones, facial bones (zygomatic arch and orbital bones), spinous processes, scapula, and ribs. Facial bones are exaggerated and eyes appear to bulge. Anus may be recessed between ischial callosities. Skin appears taut. Obvious concavity between hips and midsection. **Muscle and fat:** No muscle or fat present (causing rigid outline)	N/A	

Table 1 (Continued)

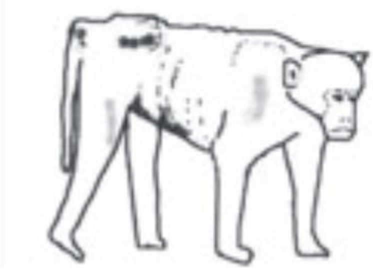
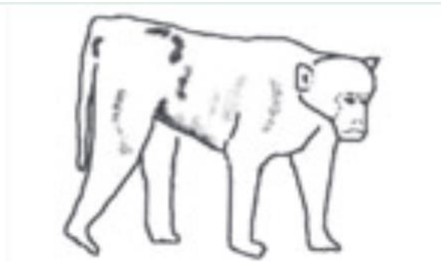
Score	Descriptor	Description	Photo	Sketch(Clingerman & Summers, 2005)
1.5	Very thin	**Body shape**: Angular, rigid body outline, below average body mass. **Morphology**: Underlying skeletal structure visible. Prominent hip bones, facial bones, spinous processes, scapula, and ribs. Face appears thin and orbits appear exaggerated. Anus may be recessed between ischial callosities. Skin appears taut. Obvious concavity between hips and midsection. **Muscle and fat**: Very little muscle, no fat present (causing rigid outline).	N/A	
2	Thin	**Body shape:** Railed like body shape, angular, thin, below average body mass **Morphology:** Prominent hip bones and spinous processes. Ribs are visible, but less prominent. Orbits appear slightly exaggerated. Skin appears taut. Obvious concavity between hips and midsection. **Muscle and fat:** Minimal fat reserves, small amount of muscle over hips and lumbar region.		

Table 1 (Continued)

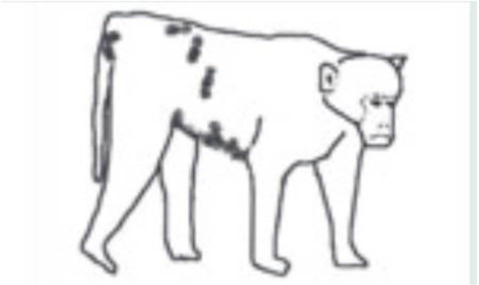
Score	Descriptor	Description	Photo	Sketch (Clingerman & Summers, 2005).
2.5	Lean	**Body shape:** Slight railed like body shape, less angular, average body mass **Morphology**: Hips and spinous processes visible, but not prominent. Ribs contours slight or absent. Moderate to slight concavity between hips and midsection. Orbits are not exaggerated; face is still slim. **Body shape**: Thin layer of fat, not obvious. Muscle appears normal.		

Table 1 (Continued)

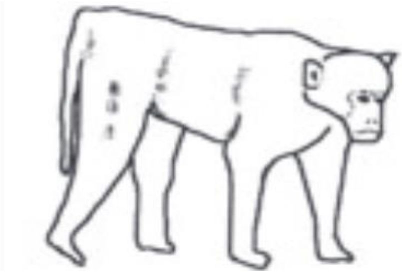
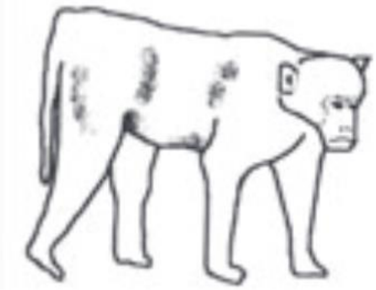
Score	Descriptor	Description	Photo	Sketch (Clingerman & Summers, 2005)
3	Optimum	**Body shape**: Smooth body shape, normal body mass **Morphology**: Hips, ribs, and spinous processes are not visible. Ribs contours are smooth. Full face, eye orbits do not protrude. Hips and midsection are very slightly or not concave. **Muscle and fat:** Well developed muscle mass and subcutaneous fat covers bones. No fat pads present		
3.5	Slightly overweight	**Body shape**: Slightly rounded but smooth body shape, normal body mass **Morphology**: Spinous processes are not visible and hips are more rounded. Rib contours are smooth. Full face, eyes do not protrude. Hips and midsection are not concave. **Muscle and fat**: Slight amounts of abdominal and lower back fat present.		

Table 1 (Continued)

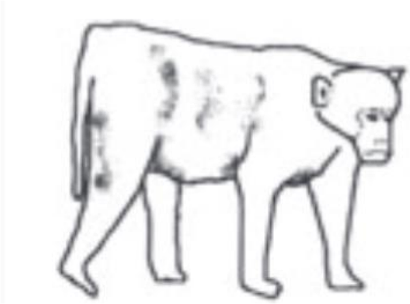
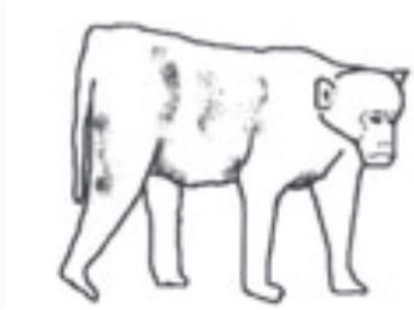
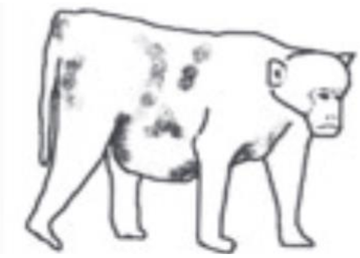
Score	Descriptor	Description	Photo	Sketch (Clingerman & Summers, 2005)
4	Overweight	**Body shape**: Rounded body shape, body less well defined, greater body mass **Morphology**: Spinous processes are not visible. Hips and lower back are rounded. Rib contours are smooth. Hips and midsection are slightly convex. Full face, eyes do not protrude. Head may appear smaller in relation to body. **Muscle and fat**: Moderate amounts of fat deposits starting to accumulate in axillary (shoulder), inguinal (groin), and/or abdominal areas.		
4.5	Obese	Body shape: Body is round, and poorly defined. Individual is 'light bulb' in shape, giving the appearance to be 'overstuffed'. Very great body mass. Morphology: Hips, ribs, and spinous processes are not visible. Abdomen/side bulge is pendulous when animal is sitting and may be present over the legs. Body is very poorly defined and convex (wide) at the hips and midsection. Head is small in relation to body. Muscle and fat: Prominent amounts of fat in abdominal, inguinal, axillary, and/or lower back regions.		

Table 1 (Continued)

Score	Descriptor	Description	Photo	Sketch (Clingerman & Summers, 2005)
5	Grossly obese	Body shape: Body is very round, and poorly defined. Individual is 'rugby ball' shaped. Extremely high body mass.		
		Morphology: Spinous processes, ribs, and hips are not visible. Body is very convex in shape and pronounced fat may alter posture. Skin rolls common.		
		Muscle and fat: Extreme fat deposits across abdominal, inguinal, axillary, and lower back regions.		

Source: (Millete et al., 2015; Clingerman & Summers, 2005)

This Study

The aim of my study was to explore mother-infant *M. fascicularis* behavior and assess their parasite load in the anthropogenic landscape of Don Chao Poo Forest, Phana, Thailand. Observational data were collected to examine intergroup variation in mother-offspring behavior and the possible effects of human activity. Fecal samples were collected from both mothers and infants to establish a basic parasite framework for this population. The following research questions were investigated regarding behavior, parasites, and body condition:

Behavior:

1a. Are there intergroup differences in maternal behaviors?

1b. Are there intergroup differences in infant behaviors?

Parasites:

2a. Do *M. fascicularis* mothers and infants at the Don Chao Poo Research Centre carry parasites? (2a)

2b. Is there intra- and intergroup variability in mother parasite count and diversity?

2c. Is there intra- and intergroup variability in infant parasite count and diversity?

2d. Is there a relationship between parasites, group road distance, and the number of human approaches per group?

Body Condition:

3a. Is there a difference in maternal body condition between groups?

3b. Is there a relationship between mother body condition and parasite load?

CHAPTER III

METHODS

Ethics Statement

This study was conducted on free-ranging long-tailed macaques. It was a non-invasive observational study and a minimum of one meter of space was maintained at all times. Approval and permission to conduct this research was granted by the Central Washington University IACUC committee (protocol # A041913). This study was funded by the generosity of Debra & Arlen Prentice, Pete and Sandra Barlow, and Central Washington University's School of Graduate Studies.

Behavior

Study subjects and site

This study occurred in the northeastern Amnat Charoen Province of Thailand at the Don Chao Poo Research Centre and Don Chao Poo Forest in the district of Phana in collaboration with the Phana Monkey Project (Figure 1). The research center is near a 300-year-old Buddhist temple where long-tailed macaques are sporadically provisioned with fruits, jasmine rice, and anthropogenic foods. The forest contains a Buddhist shrine and five groups of habituated and provisioned *M. fascicularis*. Out of the five macaque groups, I sampled four due to location and group ranging patterns, since one group traveled along a very active highway. The forest is fragmented and surrounded by busy roads in a semi-urban environment. The caretakers estimate that approximately 5-6 macaques are killed every month either from local dogs or traffic.

146 mothers and infant dyads were sampled, with a possibility of repeated sampling. Over 1000 *M. fascicularis* individuals reside within the Don Chao Poo forest. As of 2016, the estimated count was 50 dominant males, 219 young adult males, 369 females (204 mothers), 206 infants, 165 adult females, 216 sub-adult male and females, and 128 juveniles. A sterilization process of males and some females has begun to help control overpopulation at the site. These sterilized individuals have identifiable face or arm tattoos. However, I could not identify most females and non-adults of both sexes.

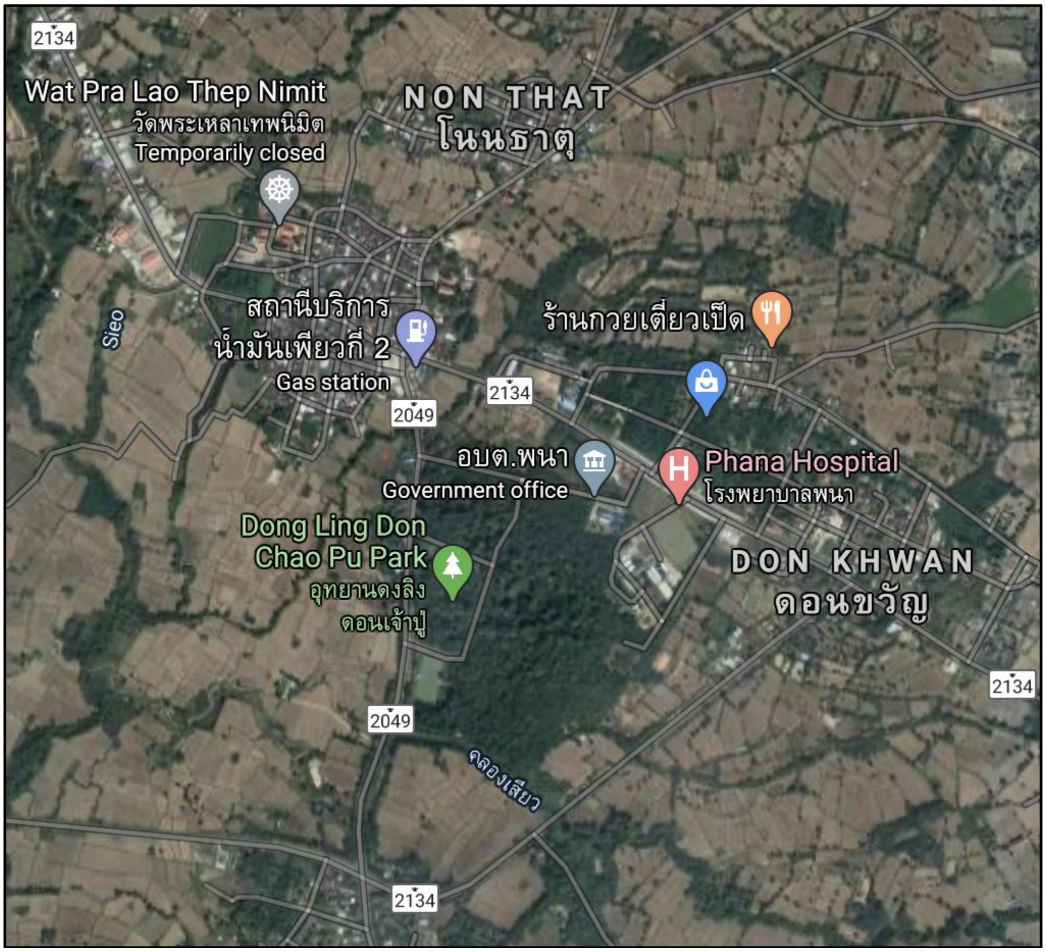


Figure 1. Map of Phana and Don Chao Poo Forest

Behavioral data collection

I followed one of the four groups each day. I identified the four different groups by their distinct sizes, identifiable individuals, and home range patterns within the forest, specifically their sleeping sites. Groups one, two, three, and four, were randomized and then followed in a randomized schedule order. I opportunistically chose mother-infant dyads from each group and referenced the dyad to previous samples based on the mother's obvious phenotypic characteristics to avoid repetition. I took the mother's photograph for each sample, which helped prevent sampling bias of the same dyad on the same day. While using my photographic library of mother identifications, I sampled dyads at random within each group. On average, I sampled three dyads each day.

I conducted 10-minute focal follows of mother-infant dyads. Behavioral follows were discarded if less than 8 minutes of behavior was not captured. Focal follows allowed for event behaviors to be recorded, as well as the duration of contact between mother and infant. Infants were identified as being attached to the mother for a higher percentage of time, possessing a smaller body size, darker coat coloration, and a pronounced mohawk or "duohawk" hair configuration. I videotaped all mother and infant behaviors (see ethogram, Table 2 and Table 3) during focal follows, which were coded with respective ethograms.

I recorded the number of non-observer human encounter rates to the group with a tally system, while I was conducting my focal follows. I calculated the groups distance using a Garmin GPS. To determine group distance, I would calculate the distance from the sampled mother-infant dyad to the road.

Table 2

Maternal Behavior Ethogram

Behavior	**Code**	**Definition**
Ventral Contact	V	Mother is seated with infant in ventral-ventral contact
Ventral Contact Grooming	VG	Mother is seated with infant in ventral-ventral contact with grooming
Ventral Contact Cradle	VC	Mother is seated with infant in ventral-ventral contact while also holding the infant tight with her hands
Cling carriage	CC	Mother actively grasps and supports infant in the ventral-ventral position while in locomotion
Passive carriage	CP	Mother is in locomotion with the infant in ventral-ventral position, but is not actively holding the infant
Retrieval	RET	Mother retrieves infant to locomote
Mother approach	MA	Mother initiates a decrease in the distance between mother and infant
Mother leaves	ML	Mother initiates an increase in the distance between mother and infant
Close Proximity	P	Mother is within one arms length of the offspring
Distant Proximity	DP	Mother is more than one arms length away from the offspring
Infant on nipple	NIP	Infant’s mouth is clasped around the mothers nipple
Nipple removal	NR	Mother removes nipple from offspring's mouth
Infant rejection	REJ	Mother denies physical contact from the infant
Weaning deterrence	WD	Mother physically denies offspring access to her nipple
Non-offspring handling	IH	An individual other than the mother touches, carries, or handles the offspring
Groom	G	Inspects or brushes fur using hands
Bite	B	Mother bites infant in punitive fashion, not associated with grooming
Restrain	RES	Mother prevents infant from moving away by holding its limb or tail
Play	P	Playful actions with other individuals
Threat face	THF	Mouth is open, eyes are wide and staring, head may be lowered
Touch	T	The mother is in contact with the infant, but is not on the ventrum or being carried
Not Visible	NV	Mother is not viewable by observer
Other	O	Any behavior that the mother presents but is not listed in the ethogram

Sources: (Dura, 2017; Maestripieri, 1994; Schino et al., 1995; Silk, 1999)

Table 3

Infant Behavior Ethogram

Behavior	**Code**	**Definition**
Ventral Contact Cling	VC	Offspring is in contact with the mother ventrally using all four limbs with the head close to the chest
Ventral Contact Hold	VH	Offspring is in contact with the mother ventrally using two to four limbs, with head not in contact to the chest
Groom	G	Offspring inspects or brushes mother's fur using hands or mouth
Play	P	Playful actions with other individuals
Offspring Approach	OA	Offspring initiates a decrease in the distance between offspring and mother
Offspring Leaves	OL	Offspring initiates an increase in the distance between offspring and mother
Close Proximity	CP	Offspring is within one meter of the offspring
Distant Proximity	DP	Offspring is distanced one meter or more away from the mother
Not visible	NV	Offspring is not viewable by the observer
Other	O	Any behavior that the offspring presents but is not listed in the ethogram
Touch	T	The infant is making contact with the mother, but is not on the ventrum or being carried

(Sources : Dura, 2017 ; Maestripieri, 1994 ; Schino et al., 1995 ; Silk, 1999).

Parasites

Fecal data collection

While collecting behavioral samples, fecal samples were collected opportunistically from infant and mother individuals. Samples were collected immediately after defecation by taking the inner part of the feces to avoid potential ground contaminants (Albani et al., 2019; Gillespie, 2006). During collection, 5 – 8 mL of feces was placed into a 15 mL centrifuge tube with a wooden (bamboo) applicator stick. New nitrile exam gloves were worn for each fecal collection to avoid cross-contamination of samples or contamination via the collector. Samples in centrifuge tubes were stored in a thermos until they arrived in the nearby laboratory, where they were processed within 30 minutes. All samples were individually marked with a sample number, substrate of collection (e.g., ground, leaf, etc.), age class, sex and time stamp when collected for later identification purposes.

Fecal processing methods

The fecal samples were analyzed for gastrointestinal parasites using both fecal flotation and sedimentation processes (Gillespie, 2006). For fecal flotation, a modified method with sodium nitrate, instead of sugar solution, was used for all samples and analyzed within the day of collection (Gillespie, 2006; Zajac and Conboy, 2012). A specific gravity of 1.2 was established with a hydrometer in the sodium nitrate solution (Zajac and Conboy, 2012). Fecal flotation floats helminth eggs and protozoan cysts, which can be reliably preserved and identified under a microscope. The parasites were photographed under the microscope with a micrometer at the largest possible magnification to measure and identify the parasite from the photograph. Fecal sedimentation was conducted with the same sample from the flotation processes. Fecal sedimentation is utilized to identify trematodes (flukes), which sink in solution instead of floating like other helminths. With a microscope, micrometer, and camera, trematodes were measured and later identified via photograph (Gillespie, 2006).

Lab protocol fecal flotation: fixed-head centrifuge

With a centrifuge tube from the fecal collection, one-third of the tube was filled with the fecal sample. Using the previously created sodium nitrate solution (with a specific gravity of 1.2), I filled the centrifuge tube with the solution leaving approximately 1inch of space from the solution to the top of the tube. I homogenized the sample with a wooden applicator stick, capped the tube, and moved the sample into the centrifuge. The sample was centrifuged at 1200 rpm for

5 minutes. The sample was removed from the centrifuge and the remaining space within the tube was filled to the rim with sodium nitrate solution creating a meniscus. A coverslip was placed onto the meniscus of solution to create a seal between the coverslip and tube. The sample stood for 10 minutes, which allowed for parasites to float to the top of the solution, and then the coverslip was removed and placed onto a labeled slide, which contained the sample number and date. The entire coverslip was examined under 10X magnification to locate parasites and then 40X to photograph and measure all parasites. To photograph the parasite, a micrometer will be placed into the microscope.

Lab protocol fecal sedimentation

The same sample from the flotation method that had already been centrifuged from the flotation method was used in this process. One beaker was covered with cheesecloth and secured with a rubber band, to prevent the cloth from slipping. The sample was homogenized with a wooden applicator stick in the centrifuge tube. The sample was then poured into diluted soapy water within a second beaker. The homogenized soapy sample from the second beaker was poured into the first beaker over a different cheesecloth. The wooden applicator stick was used to lightly strain the sample across the cheesecloth. Second straining was not necessary for these samples. After the sample was strained, the cheesecloth was discarded into a third beaker. The fecal solution was sampled with a pipette and two dots were placed onto a cover slide. Each dot was covered with a cover slip. The slide was examined under the microscope and searched for parasites with the 10x objective lens. The parasites were identified, photographed, and measured under the 40X objective lens with a micrometer and camera.

Body Condition

Body condition was scored from the video recordings and photographs using a body condition chart devised for free-ranging long-tailed macaques (Table 1) (adapted from Millette et al., 2015; Clingerman & Summers, 2005). In total, 146 mothers from the behavioral video samples were scored on a scale of 1 – 5.

Data Analysis

Data analysis was conducted using R (3.5.5) in R-Studio (1.2.5033). The following variables were examined: mother parasite count, infant parasite count, parasite diversity of mother, parasite diversity of infants, infant age, parasitic count and diversity between groups, parasitic load and diversity between groups, body condition differences, and human encounter rates. Parasite diversity was defined as the number of different genera of parasites and parasite count was defined as the number of parasites counted. A chi-square-goodness-of-fit test was run to determine if observation times were evenly distributed across groups. The data were non-normally distributed, therefore, I ran a non-parametric Kruskal-Wallis test to examine group differences in behavior and parasite count and diversity. Additionally, the Kruskal-Wallis test was used since I have three or more categorical independent groups. To determine if the number of human encounter rates, body condition, and group distance from the road affected parasite

CHAPTER IV

RESULTS

Behavior

I ran a Kruskal-Wallis test to determine if there were intergroup differences in exhibited maternal behaviors for state and event behaviors (Table 2). The following behaviors were significant: Ventral Contact (V) (Kruskal-Wallis test, $p = 0.0036$), Close Proximity (Cp) ($p = 0.0131$), Nipple (Nip) ($p = 0.0279$), Not Visible (Nv) ($p = 0.0366$), and Touch (T) ($p = 0.0275$). A post-hoc Dunn test indicated significant differences in V between the middle and shrine groups ($p = 0.0024$) and using Cohen's D index, the effect size was small ($d^a = -0.4279$); Cp between the gate and middle groups and middle and pond groups and both effect sizes were small ($p = 0.0189$, $d^a = 0.3438$; $p = 0.0248$, $d^a = -0.4717$); Nip between the middle and shrine groups ($p = 0.0167$) and the effect size was large ($d^a = 1.1137$).; Nv between the middle and shrine groups ($p = 0.0267$); and T between the middle and pond groups ($p = 0.0162$) (Table 4; Figure 2). There were significant intergroup differences using the Kruskal-Wallis test for Retrieval (Ret) ($p = 0.0009$), Mother Approach (Ma), and Mother Leaves (Ml) behaviors (Table 5). A post-hoc Dunn test indicated significant intergroup differences, including Ret between the gate and pond groups ($p = 0.0084$), gate and shrine groups ($p = 0.0138$), middle and pond groups ($p = 0.0102$), and middle and shrine groups ($p = 0,0196$). Ma differed between the middle and shrine groups ($p = 0.0117$) and the pond and shrine groups (0.0098). Ml also differed between the middle and pond groups ($p = 0.0471$) (Table 5; Figure 3).

Table 4

Intergroup Maternal State Behaviors and Their Kruskal-Wallis, Dunn, and Effect Size Values.

	State Behaviors									
	V	Cc	Cp	Dp	Nip	Ih	G	Res	Nv	T
KW p-value	**0.00361**	0.09061	**0.01313**	0.5827	**0.02793**	0.4166	0.05564	0.1871	**0.03661**	**0.02745**
Dunn Test p-value										
Gate-Middle	x	x	0.0189	x	x	x	x	x	x	x
Gate-Pond	x	x	x	x	x	x	x	x	x	x
Gate-Shrine	x	x	x	x	x	x	x	x	x	x
Middle-Pond	x	x	0.0248	x	x	x	x	x	x	0.0162
Middle-Shrine	0.0024	x	x	x	0.0167	x	x	x	0.0267	x
Pond-Shrine	x	x	x	x	x	x	x	x	x	x
	State Behaviors									
	V	Cc	Cp	Dp	Nip	Ih	G	Res	Nv	T
Cohen's D effect size										
Gate-Middle	x	x	0.3438	x	x	x	x	x	x	x
Gate-Pond	x	x	x	x	x	x	x	x	x	x
Gate-Shrine	x	x	x	x	x	x	x	x	x	x
Middle-Pond	x	x	-0.4717	x	x	x	x	x	x	-0.4071
Middle-Shrine	-0.4279	x	x	x	1.1137	x	x	x	x	x
Pond-Shrine	x	x	x	x	x	x	x	x	x	x

Small	+/- 0.2
Medium	+/- 0.5
Large	+/- 0.8

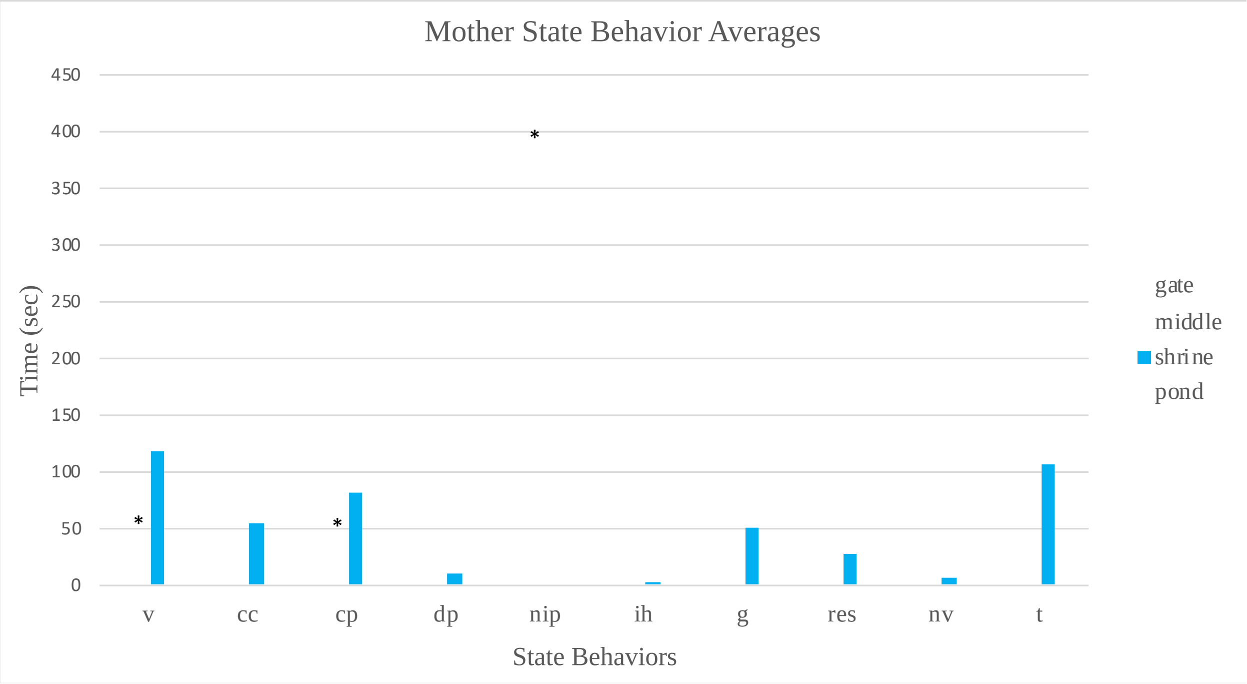


Figure 2. Mean state behaviors for mothers between groups

Table 5

Intergroup Maternal Event Behaviors and Their Kruskal-Wallis, Dunn, and Effect Size Values.

	Event Behaviors								
	Ret	Ma	Ml	Nr	Rej	Wd	B	Thf	O
KW p-value	**0.00085**	**0.01193**	**0.04212**	0.3586	0.2743	0.6225	0.3586	0.07217	0.09465
Dunn Test p-value									
Gate-Middle	x	x	x	x	x	x	x	x	x
Gate-Pond	0.0084	x	x	x	x	x	x	x	x
Gate-Shrine	0.0138	x	x	x	x	x	x	x	x
Middle-Pond	0.0102	x	0.0471	x	x	x	x	x	x
Middle-Shrine	0.0196	0.0117	x	x	x	x	x	x	x
Pond-Shrine	x	0.0098	x	x	x	x	x	x	x
	Event Behaviors								
	Ret	Ma	Ml	Nr	Rej	Wd	B	Thf	O
Cohen's D effect size									
Gate-Middle	x	x	x	x	x	x	x	x	x
Gate-Pond	-0.7121	x	x	x	x	x	x	x	x
Gate-Shrine	-0.5353	x	x	x	x	x	x	x	x
Middle-Pond	-0.4472	x	0.2462	x	x	x	x	x	x
Middle-Shrine	-0.2704	-0.4786	x	x	x	x	x	x	x
Pond-Shrine	x	0.4786	x	x	x	x	x	x	x

Small	+/- 0.2
Medium	+/- 0.5
Large	+/- 0.8

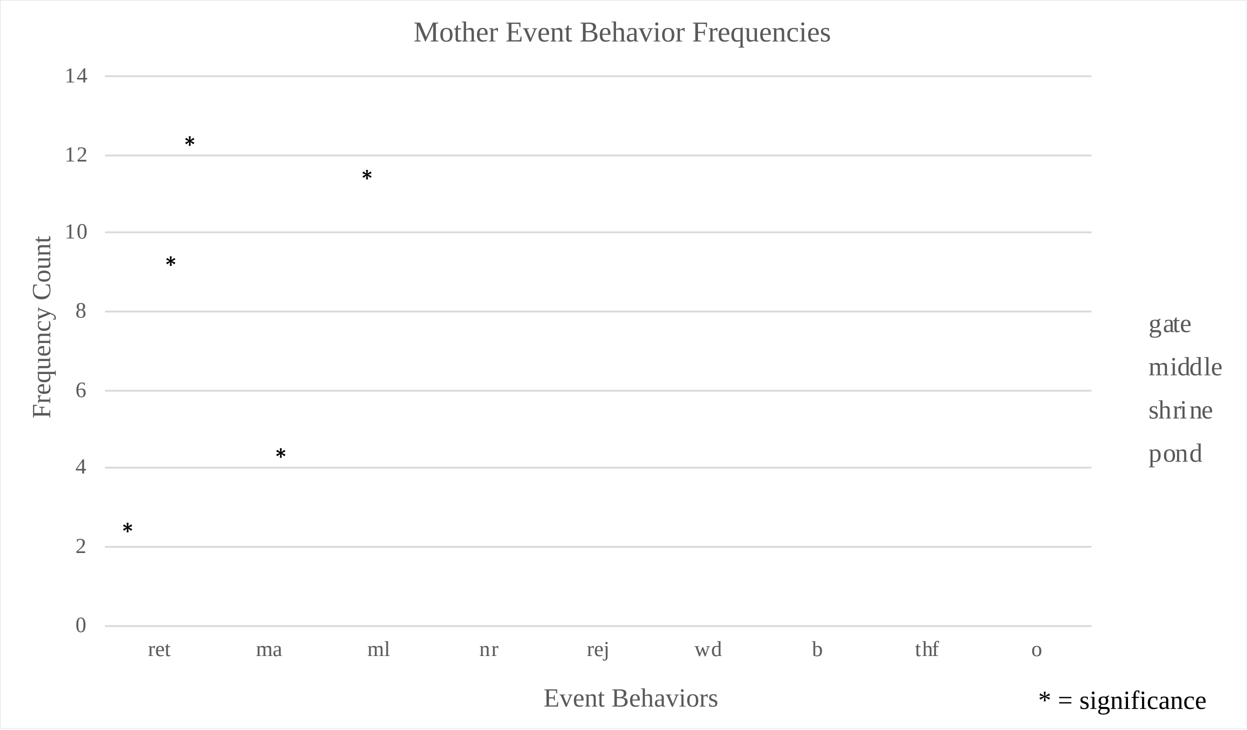


Figure 3. Event behavior frequencies for mothers of different groups

To determine whether infant behaviors (Table 3) were significantly different between groups, I ran a Kruskal-Wallis test. No event behaviors were found to be significant. The following state behaviors were significant ($p < 0.05$): Close Proximity (Cp), Nipple (Nip), and Touch (T). I ran a post-hoc Dunn test to determine which groups had significant differences: Cp behavior differed between the gate and middle groups; Nip behavior differed between the gate and shrine and middle and shrine groups; T behavior differed between the gate and middle, middle and pond, and middle and shrine groups (Table 6; Figure 4).

Table 6

Infant Behaviors and Their Kruskal-Wallis, Dunn, and Effect Size Values.

	State Behaviors								Event Behaviors	
	Vc	Vh	G	Cp	Dp	Nv	Nip	T	Ol	O
KW p-value	0.7739	0.06298	0.2576	**0.04326**	0.585	0.4435	**0.01524**	**0.002869**	0.1718	0.741
Dunn Test p-value										
Gate-Middle	x	x	x	0.0325	x	x	x	0.0085	x	x
Gate-Pond	x	x	x	x	x	x	x	x	x	x
Gate-Shrine	x	x	x	x	x	x	0.0398	x	x	x
Middle-Pond	x	x	x	x	x	x	x	0.0045	x	x
Middle-Shrine	x	x	x	x	x	x	0.0141	0.0012	x	x
Pond-Shrine	x	x	x	x	x	x	x	x	x	x

	State Behaviors							
	Vc	Vh	G	Cp	Dp	Nv	Nip	T
Cohen's D effect size								
Gate-Middle	x	x	x	0.6258	x	x	x	0.8959
Gate-Pond	x	x	x	x	x	x	x	x
Gate-Shrine	x	x	x	x	x	x	0.1206	x
Middle-Pond	x	x	x	x	x	x	x	-1.0883
Middle-Shrine	x	x	x	x	x	x	-0.1503	-1.4761
Pond-Shrine	x	x	x	x	x	x	x	x

Small	+/- 0.2
Medium	+/- 0.5
Large	+/- 0.8

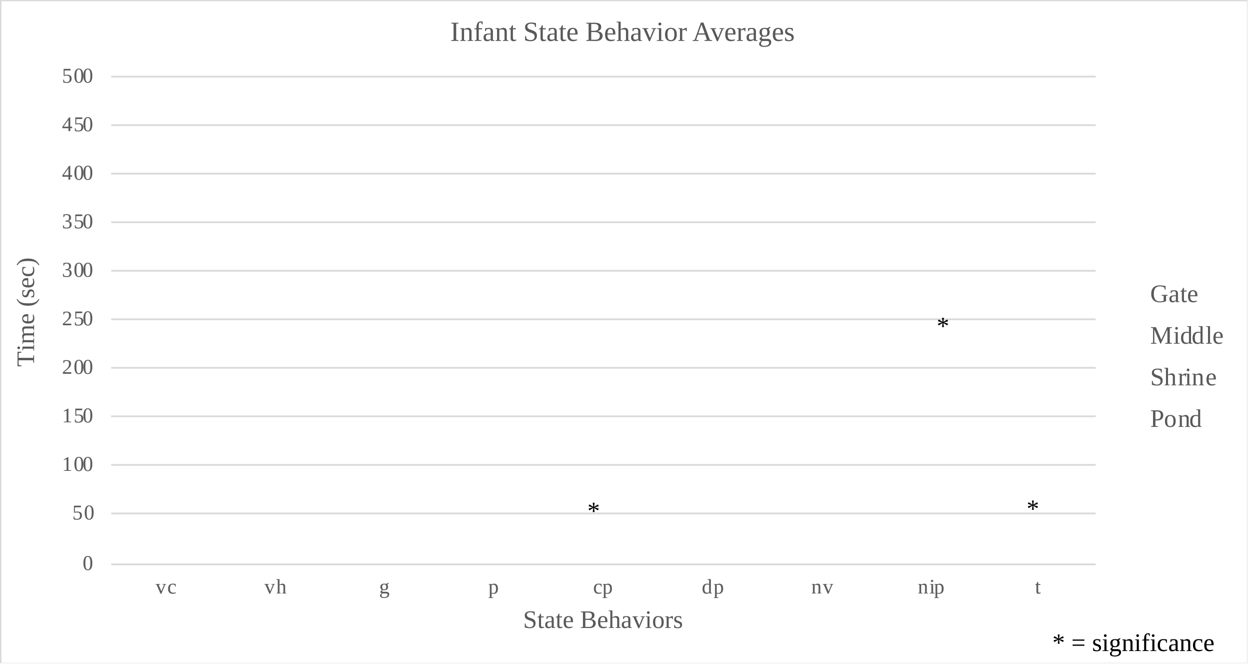


Figure 4. Mean state behaviors for infants between groups

Parasites

T The sampled mothers and infants (n = 40, 10 samples per group) at Don Chao Poo Forest carry parasites. Overall, 1586 eggs, 146 worms/larvae, 56 protozoa, and 67 unidentified parasites were counted (Table 7) in the samples (Figure 5). The mean parasite diversity for all samples was 3.975 parasites, and the mean parasite count for all samples was 46.350 parasites. The overall parasite count and diversity did not differ significantly between groups (Kruskal-Wallis, total count: $\chi^2 = 0.886$, df = 3, $p > 0.05$, diversity: $\chi^2 = 0.610$, df = 3, $p > 0.05$) (Table 8). Parasite count was highest in the middle group (768, mean = 32.5) followed by the pond (492, mean = 76.800), gate (325, mean = 26.900), and lastly the shrine group (269, mean = 49.200). The highest parasite diversity was in the pond group (8) followed by the gate group (4), and then the middle (6) and shrine (6) groups.

Table 7

Parasite Diversity and Their Associated Counts

Parasite	**Count**
Strongylida fam. gen. egg	1068
Anclyostoma sp. egg	392
Trichuris sp. egg	63
Ascaris sp. egg	39
Mammomonugamus egg	4
Toxocara sp. egg	14
Isospora sp. egg	3
Hymenolopis sp. egg	3
Strongylida fam. gen. larvae	58
Strongylida fam. gen.	61
Anclyostoma sp.	24
Trichuris sp.	3
Enterobius sp.	10
Balantoides sp.	10
Entamoeba spp.	4
Giardia sp. cyst	28
Chilomastix sp.	4
Unidentified	67

Table 8

Individual, Group, and Age Class Parasitic Counts, Diversity, Mean, and Ranges.

	Mother Parasite Load		Infant Parasite Load	
Group	**Total**	**Diversity**	**Total**	**Diversity**
Gate	8	3	10	5
Gate	5	3	55	7
Gate	4	2	70	6
Gate	13	4	12	3
Gate	100	4	48	3
MEAN	*26*	*3.2*	*39*	*4.8*
RANGE	*96*	*2*	*60*	*4*
Middle	12	5	16	2
Middle	14	6	8	2
Middle	4	2	651	5
Middle	13	3	19	6
Middle	5	2	26	4
MEAN	*9.6*	*3.6*	*144*	*3.8*
RANGE	*10*	*4*	*643*	*4*
Shrine	29	6	5	2
Shrine	10	4	31	3
Shrine	5	3	13	6
Shrine	29	5	8	5
Shrine	30	3	109	5
MEAN	*20.6*	*4.2*	*33.2*	*4.2*
RANGE	*25*	*3*	*104*	*4*
Pond	1	1	1	1
Pond	18	8	8	2
Pond	5	3	0	0
Pond	24	7	331	8
Pond	78	7	26	3
MEAN	*25.2*	*5.2*	*73.2*	*2.8*
RANGE	*77*	*7*	*331*	*8*

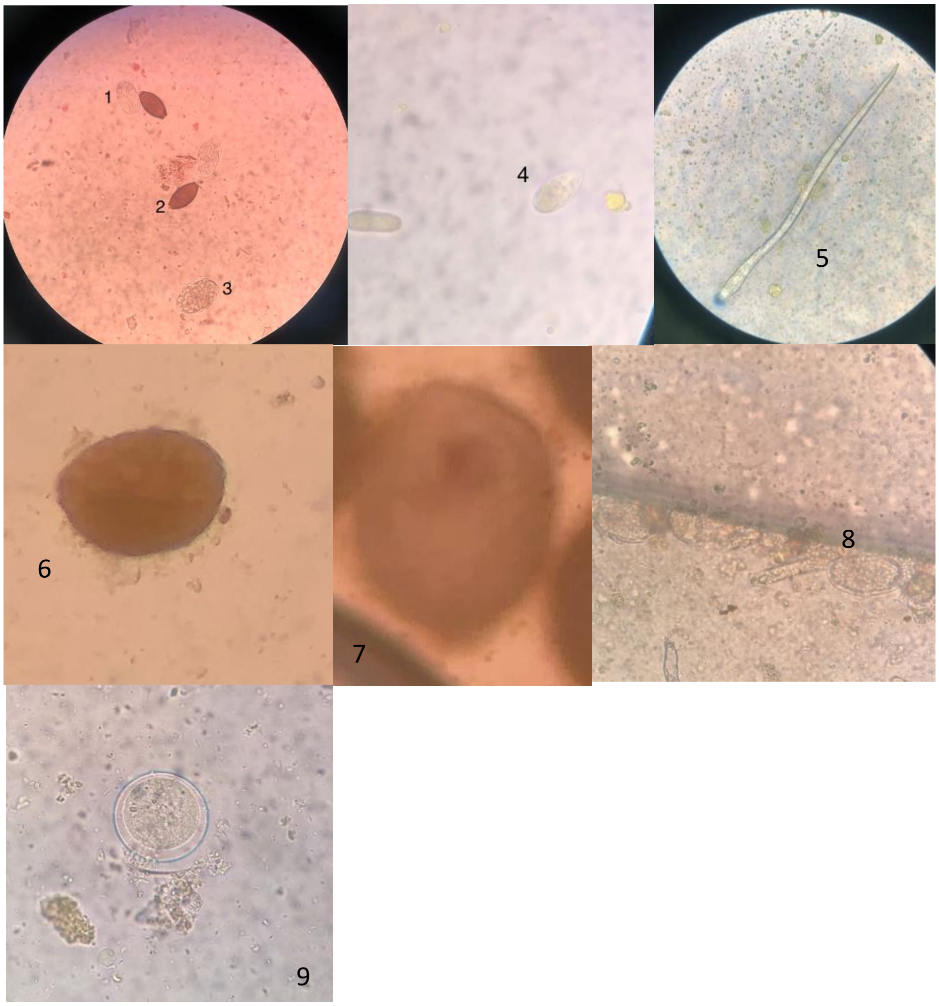


Figure 5. Common parasites from Don Chao Poo Forest: 1. *Strongyloides* egg, 2. *Trichuris* egg, 3. *Anclyostoma* eff, 4. *Enterobius* egg, 5. *Stronyloides* worm, 6. *Balantoides*, 7. *Chilomastix*, 8. *Ascaris* egg, 9. *Entamoeba*

There was no significant difference in parasite load between mothers of the different groups (Kruskal-Wallis, parasite count: $\chi^2 = 1.720$, df = 3, $p > 0.05$, diversity: $\chi^2 = 2.211$, df = 3, $p > 0.05$) (See Appendix D for intra- and inter parasitic variation; Table 8). The mothers of the gate group (n = 5) had a mean parasite count of 26 (range, 96) and mean parasite diversity of 3.2 (range, 2), the middle group (n = 5) had a mean parasite count of 9.6 (range, 10) and mean diversity of 3.6 (range, 4), the shrine group (n = 5) had an mean of 20.6 (range, 25) parasites and mean diversity of 4.2 (range, 3), and the pond group (n = 5) had an mean parasite count of 25.2 (range, 77) and mean diversity of 5.2 (range, 7) (Appendix D; Table 8).

There were no significant intergroup differences between infant parasite loads (count: $\chi^2 = 1.879$, df = 3, $p > 0.05$, diversity: $\chi^2 = 2.2107$, df = 3 $p > 0.05$) (Appendix D). The infants of the gate group (n=5) had a mean parasite count of 39 (range, 60) and a mean parasite diversity of 4.8 (range, 4). The infants of the middle group (n = 5) had a mean parasite count of 144 (643) and a mean parasite diversity of 3.8 (range, 4). The shrine group infants (n = 5) had a mean parasite count of 33.2 (range, 104) and a mean parasite diversity of 4.200 (range, 4). The pond group infants (n = 5) had a mean parasite count of 73.2 (range, 331) and mean parasite diversity of 2.8 (range, 8) (Table 8, Appendix D).

Parasite loads only significantly differed within group mother and infants in the middle group (Kruskal-Wallis and Dunn test, count: $p = 0.047$). The mother-infant parasite counts and diversity for all other groups were not significantly different (Kruskal-Wallis, $\chi^2 = 3.938$, df = 1, $p > 0.05$) (Table 8).

There were weak relationships observed between body condition and parasite count and body condition and diversity (Spearman’s correlation, $r = 0.1666$, $r = -0.3798$, respectively). The gate group had the most human approaches (272 people), followed by the middle (226 people), pond (186 people), and shrine groups (156 people) (Table 9). The gate group was on average, the closest to the road (0 m), followed by the middle (115 m), pond (136 m), and shrine group (230 m) (Table 9). There was a weak relationship between parasite load and the number of human approaches (Spearman’s correlation, $r = 0.1088$) as well as group distance from the road and the number of parasites (Spearman’s correlation, $r = -0.0919$) (Table 9). There was a strong negative relationship between group distance to the road and the number of human approaches

(Spearman’s correlation, r = -0.9708947) (Table 8). There were weak relationships observed between body condition and parasite count and body condition and diversity (Spearman’s correlation, r = 0.1666, r = 0.3798).

Table 9

Number of Group Approaches, Mean Group Distance to the Road, and Parasite Counts for the Four Groups.

Group ID	Distance to Road (m)	Human Approaches	Parasite Count
Gate	0	272	325
Middle	115	226	768
Shrine	230	156	269
Pond	136	186	492

Body Condition

A mean of 36.5 focal samples were obtained across all four groups (n = 36, pond, gate, shrine; n = 38, middle) (Table 10). I ran a Kruskal-Wallis test to determine whether the body condition of mothers differed between groups. Body condition differed between at least two groups (χ^2 = 132.29, df = 3, p > 0.05, p < 0.001) (Table 10; Figure 6). A post-hoc Dunn test indicated differences between the pond and gate group (p < 0.001) , the pond and middle group (p < 0.001), and the pond and shrine group (p < 0.001) (Table 10; Figure 6). Cohen’s d effect size reported that the pond and gate group had a negligible effect size (d^a = -0.1956), the pond and middle group had a large effect size (d^a = 0.9612), and the pond and shrine group had a small effect size (d^a = 0.4807).

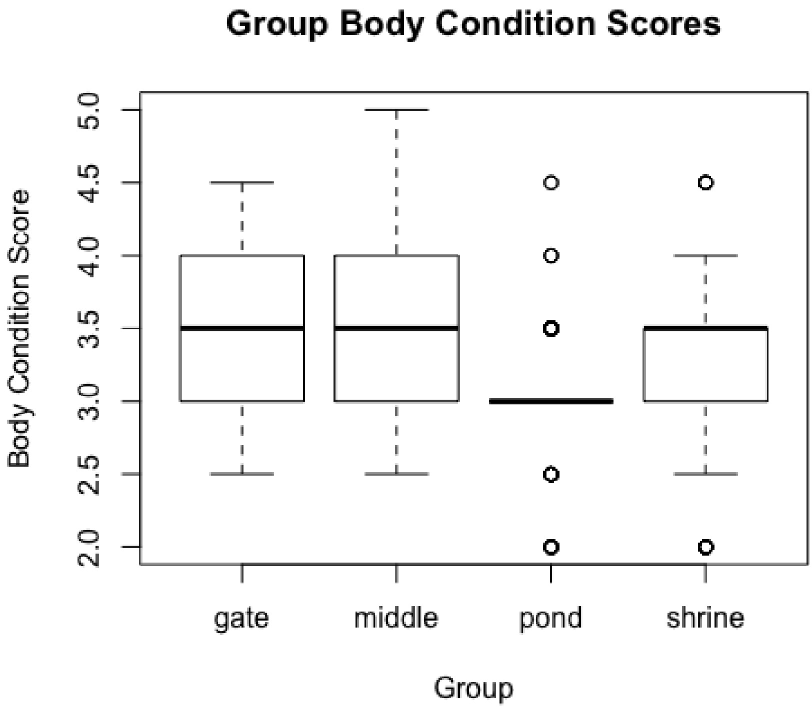


Figure 6. Group body condition scores

Table 10

Mother Body Condition Scores

	Body Condition Scores						
	2	**2.5**	**3**	**3.5**	**4**	**4.5**	**5**
Gate	0	1	15	8	11	1	0
Middle	0	3	10	14	8	2	1
Shrine	2	1	12	13	7	1	0
Pond	2	8	19	5	1	1	0

CHAPTER V

DISCUSSION

Behavior

Maternal behavior

I aimed to explore the mother-infant relationships between four groups of long-tailed macaques in an anthropogenically effected forest. Maternal behaviors of ventral cling, close proximity, nipple, not visible, touch, retrieve, mother approach, and mother leave all differed significantly between groups. Nipple was the most common behavior followed by touch and ventral cling. These behaviors were expected to occur at high frequencies based on the classification of mothers and infants (i.e., an infant was attached to the mother for a higher percentage of time) (Schino et al., 1995). The middle group was significantly different from all other groups for the significant state behaviors suggesting that the middle group mothers were interacting with their infants differently. The middle group also had the second highest amount of human approaches, the highest body condition scores, and the lowest parasite count. These biological factors could also influence the differences in group behavior.

Retrieve, mother approach, and mother leave were all significantly different event behaviors between groups. The mothers of the pond group retrieved their infants the most and exhibited the highest frequencies of threat face. This suggests that the mothers had more aggressive encounters with other individuals and/or the mothers I sampled were all relatively lower ranked (Altmann & Alberts, 2005). Mothers approached their infants the most in the shrine and gate groups compared to the pond and middle groups. The gate mothers might have been more vigilant of their infants based on the number of human approaches, which was highest in the gate group, suggesting that human activity could be one reason for mother behavioral differences in this group (Dore, Riley, & Fuentes, 2017). The high frequency of retrieve, mother approach, and mother leave in the shrine group remains unexplained. Mothers left their infants more frequently in the middle group compared to the other three groups. One explanation might be that the middle group mothers were more motivated to investigate humans and retrieve their resources. The middle group had a relatively high amount of human approaches and had the highest body condition scores, suggesting they might come in contact with unnatural foods more frequently (Loudon, Howells, & Fuentes, 2006). Furthermore, the middle mothers high body condition scores, and thus might have allowed them to produced richer milk and leave their infants on the nipple longer and parked more often. However, the middle group mothers only left their infants four more times than the pond group (Figure 3). This behavioral difference could be from one mother and might not be indicative for the group as a whole, because mothers were opportunistically sampled and individual IDs were unknown.

Differences in maternal group behavior can be attributed to multiple variables that were not all quantifiable in this study. Human approaches, mother’s age, and rank were not determined to effect behavior (Dore et al., 2017; Schino et al., 1995; Gomendio, 1990). Furthermore, the population density was so high within this forest that the expected despotic long-tailed macaque social structure could be destabilized. Group size can influence mother-infant relationships. In *M. mulatta*, as group size increased, so did the proportion of time the infant spent in proximity the mother (Berman et al., 1997). In contrast, in *M. mulatta* and *M. fuscata*, mothers in larger groups spent less time in contact with their infant, but initiated and spent more time in proximity to their infant (Liu et al., 2018; Schino et al., 1995) Notably, groups exhibited different amounts and frequencies of maternal behaviors, suggesting that group composition and human activity could be specific to certain areas of the park, related to group size, or how the macaques socially organize themselves.

Infant behavior

Infants only significantly differed in state behaviors, including close proximity, nipple, and touch. Close proximity was significantly higher in the gate group compared to the middle group. The infants were either younger and less adventurous or their mothers stayed closer to them for safety. Mothers in the gate group approached their infants more frequently, so close proximity in infants was most likely related to their mothers' increased vigilance (Gochfeld & Burger, 1994). This most likely occurred because the gate group received the most human approaches and were closest to the road, where increased vigilance from threats (e.g., cars and dogs) was needed for infant safety (Gochfeld & Burger, 1994). The shrine group infants spent significantly less time on the nipple than the middle or gate groups. The infants of the shrine group spent more time attached ventrally compared to other groups. The infants of the shrine group were possibly older and needed to spend less time feeding with their mother. The middle and gate group infants spent the most time on the mother, suggesting that these infants were younger or other food resources were less available or less appealing to them. The shrine group spent most of its time in the forested area behind and next to the shrine, whereas the middle and gate groups spent a large portion of their time on the concrete walkways or in the shrubbery. Humans would most often offer food to the macaques at the entrance of the park, usually due to the swarming effect the macaques created for anyone who entered the gates with food. Young infants usually did not partake in eating the human offered food unless it was fruit. Lastly, touch behavior was significantly lower in the middle group compared to the other three groups. The infants of the middle group spent a large portion of their time on the nipple and ventral area and a low amount of time in away from but in proximity to their mothers.

Parasites

Overall, 39 of the 40 fecal samples collected had identifiable parasites. From this baseline data, we can assume that most monkeys at the Don Chao Poo forest carry parasites. This study took place in July and August, and parasite prevalence is influenced by season, thus certain parasitic data may be variable throughout the year (Modry et al., 2018). The macaques are likely to be acquiring parasites from stagnant and/or water sources or contaminated food. Due to the population's high density, the parasites are more likely to flourish within the environment. The identified parasites had similar overlap with other studies researching free-ranging macaques. A parasite study conducted on *Macaca maura* in a disturbed habitat on Sulawesi shared six of the identified parasites from Don Chao Poo, including *Trichuris sp*., Strongylida fam gen., *Balantoides sp., Entamoeba sp., Chilomastix sp., and Giardia sp*. (Albani et al., 2019). Additionally, the long-tailed macaques of Don Chao Poo shared many of the same parasites that were identified in long-tailed macaques in Bali at religious sites with high rates of human contact(Lane et al., 2011) including Anclyostoma sp., Ascaris sp., Trichuris sp., Entamoeba sp., Enterobius sp., Giardia spp., Isospora spp., and Balantidium spp. (Lane et al., 2010). Similar parasites were observed in *Colobus guereza* and *Piliocolobus tephrosceles* living on the forest edge in Kibale National Park (Chapman et al., 2006). The high number of parasites found within my dataset at Don Chao Poo in certain individuals (e.g.,651, 331, 109) is concerning, and based on previous research, could have pathological consequences (Loker & Hofkin, 2015). Additionally, many species of the parasites I identified, such as *Mammoganamus* sp. and

Hymenolepis sp. have been confirmed in other parasitic studies on alloprimate species (Modry et al., 2018), and *Trichuris sp., Mammomonugamus sp., Toxocara sp., Giardia sp., Strongyloides sp*., and *Anclyostoma sp*. are commonly found in domestic dogs and cats (Zajac & Conboy, 2012). The monkey's parasite load at Don Chao Poo could be influenced by zoonotic transmission from domestic animals. Moreover, almost all free-ranging vertebrates have some kind of documented parasitic infection, so it is possible that human activity in Don Chao Poo could not be heavily impacting the macaque's parasite load at Don Chao Poo Forest.

The identified parasite diversity within the macaques (Table 7) at low prevalence causes only mild gastrointestinal symptoms. Whipworm (*Trichuris sp*.) infections are asymptomatic when light, but heavy loads can result in painful stool and rectal prolapse (Modry et al., 2018). Multiple individuals within the sampled groups had a high number of whipworms present, when compared to other free-ranging macaque parasite studies, and could experience distress while defecating (Table 8). *Strongyloides sp.* infections can be acute or chronic (Modry et al., 2018; Viney & Lok, 2015). The acute form presents itself as a rash upon initial penetration of the worm into the skin. Tracheal irritation and dry cough can also occur when the larvae migrate from the lungs into the trachea, so they can be swallowed into the digestive tract (Modry et al., 2018). When swallowed, the larvae can cause gastrointestinal distress including diarrhea, constipation, abdominal pain, and anorexia. Chronic *Strongyloides sp.* infections are also mostly asymptomatic (Viney & Lok, 2015). The Strongylides count was high in the macaques sampled at Don Chao Poo when compared to other macaque parasite studies. Ascaris sp. infections are often asymptomatic, light infections cause mild abdominal discomfort, and heavy infections can cause intestinal blockage and even impair development (Modry et al., 2018). Ascaris sp. can be acquired from the soil or from feces of another infected individual (Modry et al., 2018).

Ancylostoma, or the hookworm, can cause a variety of symptoms including abdominal pain, nausea, anorexia, and iron deficiency in heavy infections (Modry et al., 2018). *Anclyostoma sp.* also causes a dermal reaction (ground itch) from the filariform larvae (Modry et al., 2018). The *Anclyostoma* infections were high in the monkeys of Don Chao Poo Forest. Giardia sp., a protozoan, can be asymptomatic, but commonly causes diarrhea, soft stool, upset stomach and cramps, as well as dehydration (Modry et al., 2018). *Hymenolepis nana* infections are usually mild or asymptomatic, but in young individuals, it can cause sever intestinal symptoms (Heyneman, 1996). Serious infections can cause malabsorption of nutrients and weight loss. *Hymenoloepis* is uncommonly found in macaques, but are commonly found in humans and some ape species.

From the parasite species specific group differences, we can postulate that the sampled individuals in certain group will be more or less likely exhibit certain pathologies. *Toxocara* pathology could more likely be found in the middle group, *Enterobius* in the shrine group, *Giardia* in the gate group, *Chilomastix* in the middle group, and *Trichuris* in the pond group.

Mother Parasites

None of the mother parasite loads were significantly different, but this may be due to the small sample size. For example, the mean parasite count for three groups (gate, shrine, and pond; 26, 20.6, and 25.2, respectively) was high, but the middle group value was low (9.6), which could be due simply to the individuals sampled. Alternatively, the middle group could have an overall lower parasite count due to an increased immunity to certain parasites or a more naturalistic diet (Mabbott, 2018). The middle group also had a low parasite diversity (3.6), especially compared to the highest average diversity of 5.2 from the pond group. The low parasite diversity of the middle group could also suggest a higher immunity to certain parasites compared to the other groups (Mabbott, 2018). Although the gate group had the highest parasite count average of 26, their average parasite diversity was lowest (3.2). An explanation for this makes sense at the individual level: one mother had a total parasite count of 100, whereas the other mothers' counts ranged between 4 and 13. Without this outlier mother, the average parasite count for the gate group mothers would be 7.5 parasites per individual, making it the least parasitized group. Therefore, outliers are important to consider. A high parasite count in one individual could be indicative of a larger distribution within a group, especially when "super-group" sizes consist of approximately 200 individuals. This individual could be older and have a weakened immune system, be a central component of a grooming network and receive more contact than others, or has more contact with contaminated resources and/or people (Mabbott, 2018; MacIntosh et al., 2012). The mothers of the pond group had the highest mean diversity and second highest mean parasite count (5.2 and 25.2, respectively). This group might be highly parasitized due to resource access. The pond group resides in a section of the park that is not frequently cleaned by the park caretakers. Rotting fruit and other human foods, such as candy, noodles, and chips, sit on the ground for approximately four days before removed by caretakers or rain. Interestingly, the pond group had the third lowest rate of human approaches. The reasons for parasitic variation in this population are unknown, although groups that had high encounter rates seemed to have a more controlled parasite prevalence in mother macaques. More research is needed to understand intergroup variation, which could help explain why some individuals have a high parasite load and why some groups have fewer parasites than others.

Infant Parasites

None of the group parasite loads of the infants were significantly different. Similar to the mothers, individual variability could help explain adult health trajectories and infant health differences. Consistent with previous research, infants had a higher parasite load than mothers (Souchay et al., 2013; Kelly & Janz, 2008). The middle group had the highest parasite count (mean of 144 parasites), particularly because of one outlier infant (parasite count of 651). This extremely high parasite load is concerning because such a load can result in mortality (Hilser et al., 2014). Specifically, this infant was predominantly afflicted with strongylids which is common and found in mammals (including humans), amphibians, reptiles, and birds (Viney & Lok, 2015). The presence of a strongylid is not serious, and the pathology is mild, affecting the abdominal, respiratory, and skin areas. With such a high number of worms, death can occur via diarrhea and constipation (CDC, 2018). The transmission of a strongylid is versatile, as it can be acquired through fecal-oral contact and can be free living and attach itself to a host opportunistically (CDC, 2018; Viney & Lok, 2015). Excluding this individual, the mean parasite count for the middle group would be 17.25, which would be the lowest group count overall. Although this infant had the highest parasite count overall, infants in other groups had parasite counts above 100 (infant in shrine group = 109; infant in pond group = 331). High parasite counts across multiple individuals and multiple groups suggests that other infants in the population are likely afflicted with high parasite counts.

All infants with a parasite count over 100 also had a parasite diversity of ≥ 5. The lowest recorded diversity from any individual was 0 and was recorded in the pond group. Similar to the mothers, the infants of the pond group had the second highest mean parasite count and without the individual with 331 parasites present, they would have the lowest parasite mean.

Unlike the mothers in the pond group, their group diversity was low. The pond group parasites were most likely acquired through dietary differences, and because infants spend a large portion of time nursing, they might eat less food infected by pathogens. Notably, I noticed multiple infants still on the nipple partaking in eating human-offered food, mostly fruit. The gate group infants had the highest parasitic diversity and the most human approaches, which could explain why they had more species present (Lazdane, Broll, Theisinger, Bearder, & Donati, 2014). Furthermore, the gate group spent a large portion of their time on the road and sitting in residential areas across the park. The possibilities of increased domestic animal and human contact from being in proximity to the road could also explain high parasitic diversity (Lazdane et al., 2014). Infants have minimal to no immunological defenses against parasites, and more focus should be given to the acquisition of parasites and development on parasitic immunity in young individuals (Mabbott, 2018; Souchay et al., 2013; Kelly & Janz, 2008).

Intergroup Differences

Parasite counts only differed between mother and infant samples in the middle group. The high parasite count in infants in this group could translate to successful immunity in adulthood (Mabbott, 2018). Although only a trend, infant parasite count was higher than the mothers in every group, which was expected. Infant parasite diversity was more variable but was only lower than the mother's parasite diversity in the pond group. Differences in parasite load were greater in the infants compared to the mothers, expressing greater variability within the infant population.

Anthropogenic Effects

Parasite load was not related to group road distance or the number of human approaches. The gate group received the most approaches followed by the middle, shrine, and pond groups (Table 9). Distance to the road and the number of human approaches were related. The shrine group was the furthest from the road because they spent much of their time behind the shrine and in the trees. The other three groups spent a large portion of their day on the sidewalks and in the lower vegetation near the edge of the forest.

The relationship between the groups and human approaches remains unknown. Does distance to the road and the number of approaches impact groups differently in a small forest with such a high population density? For instance, the monkeys tended to congregate together when large food donations were made. How much dietary and spatial overlap occurs over a longer period of time? Future research should incorporate a larger sample size on space use, human food consumption, human approaches, and human contact rates to understand the complexity of macaque health in small religious parks, such as Don Chao Poo Forest.

I selected mothers and infants to sample for multiple reasons. First, mothers with infants are more easily identifiable. Additionally, in Macaca, a female's position within a grooming network is correlated with certain parasitic infection rates (MacIntosh et al., 2012) and offspring spend a large proportion of their time playing socially (Wright, Mayhew, Sheeran, Funkhouser, & Wagner, 2018) and in direct contact with their mother (Dura, 2017). Offspring have been shown to carry significantly more parasites than other age classes (Souchay et al., 2013; Kelly & Janz, 2008; Nunn & Altizer, 2006); therefore, mothers are at a greater risk for parasitic infection due to their offspring acting as a vector. It is important to note that the sample size in this study was small, and individual variation is crucial to understand within the group setting. These samples should be seen as preliminary indicators for this particular population.

Body Condition

No relationship was established between body condition scores and parasite load. Body condition scores are useful to determine nutritional status in this population (Millette et al., 2015; Clingerman & Summers, 2005). The middle group had the highest body condition scores, suggesting they eat higher amounts of unnatural food. The middle group mothers also had the lowest parasite count, and relatively low parasite diversity. This could support that the middle group has a greater immunity to parasites in adulthood due to the high contact rate from humans and unnatural foods (Graczyk et al., 2002, Köndgen et al., 2008). The gate group had the most similar body condition scores to the middle group and a similar parasitic diversity to the middle group. The pond group had the highest parasite diversity and the lowest body condition scores. The pond group could have an older mother population and/or has less or worse food and water resources (Clingerman & Summers, 2005).

A tool to assess free-ranging alloprimate body condition has only been established for lemurs (Millette et al., 2015). Previous body condition scales have been established for M. mulatta but only in a laboratory setting (Clingerman & Summers, 2005). I wanted to create a tool to understand body condition in free-ranging long-tailed macaques and explore body condition variability between groups. Body condition is an important health indicator and is a subjective method of assessing body fat and muscle (Burkholder, 2000). Specifically, a body condition scale can be useful in understanding nutritional adequacy and the consequences of diet on the individual, group, or population (Clingerman & Summers, 2005). Furthermore, extreme body condition scores may predict or correlate with certain diseases or conditions (Clingerman & Summers, 2005). I sampled 146 mothers based on their body condition and determined their scores. Body conditions differed between groups. Specifically, the pond group had significantly lower body condition scores than the three other groups. One possibility for why these 38 mothers had lower scores could be related to differences in group diet, overall health, or a bidirectional relationship between the two (Clingerman & Summers, 2005). The middle group had the highest body condition scores (one individual scored a 5, which is characterized as grossly obese) and was significantly different from the pond group. The pond and shrine groups had individuals characterized as thin (body score = 2), and more mothers in the pond group had lower scores. The pond group scored significantly differently from all three groups.

The Don Chao Poo forest is small (approximately 1.44 mi2 or 373 hectares) and contains more than 1000 long-tailed macaques, surrounded by busy roads, and has daily visitors for tourist and religious reasons. The forest abuts the small town of Phana, rice paddy fields, and a highway. During my eight-week study, I counted over 800 human approaches to the macaque groups. Previous research shows that habitat loss and fragmentation have affected host susceptibility to parasite infection in wild primate populations (Albani et al., 2019; McCallum 2008). Furthermore, when a population is unable to disperse or leave unsuitable habitats due to fragmentation, parasites that are transmitted via the fecal-oral route flourish due to an increase in host density and can enhance socially and environmentally mediated infection risks (Gillespie and Chapman, 2008). From this spatial constraint, we can predict that the parasite load should be higher in disturbed and fragmented areas (Lazdane et al., 2014). Similarly, the transmission of parasites often occurs when there is a high density of both human and wildlife populations that share resources (e.g., a religious forest) (Daszak & Cunningham, 2003; Daszak, Cunningham, & Hyatt, 2001; Fuentes et al., 2005). Primates that live near forest edges also have a higher likelihood of encountering humans, non-forest dwelling species, and have increased zoonotic pathogens (Hussain et al., 2013). In Bali, all temple living macaques are known to have gastrointestinal parasites, but the macaques with higher parasite burdens are found at temples surrounded by more anthropogenically disturbed land (Lane-DeGraff et al., 2014). Furthermore, the temple with the largest macaque population in Bali has approximately 600 long-tailed macaques, whereas Don Chao Poo has more than 1000. All of the environmental and fragmentation constraints noted in previous research applies to the macaques at Don Chao Poo Forest and suggests concern is necessary about the population's health and parasite load. Parasitic diversity and count assessment are imperative to understand the ecological threats within the population.

Though parasites are abundant across vertebrate species and can vary in host impact from mild to asymptomatic, parasitism can often induce detrimental consequences to their hosts via alterations in nutritional intake, immune function, and metabolism (O'Donnell, 1997). Many parasites divert nutrients to themselves, which can cause adverse consequences, such as host weight loss (Loker & Hofkin, 2015). A common parasite in alloprimates, Giardia lamblia, can adhere to the microvilli of the intestines and can interfere with nutrient absorption (Loker & Hofkin, 2015). Parasites can also enter the host and can trick your body into creating a damaging immune response, which can lead to severe infection that can have detrimental consequences. For instance, parasites can employ antigenic mimicry or antigenic variation, occupy immune privileged sites, and can avoid destruction by host cells (Loker & Hofkin, 2015). Furthermore, parasites can cause physiological damage (Loker & Hofkin, 2015). For instance, tape worms create large cyst-like structures in the tissues and organs of their intermediate host, Plasmodium infections cause iron deficiency, and Schistosoma and Trichinella can cause metaplasia, all have been identified in various alloprimate species (Modry et al., 2018; Loker & Hofkin, 2015). Due to the high population density and parasitic diversity within Don Chao Poo, the physiological consequences of parasites are likely to impact this population.

Parasites can also be indicators of and effect population structure (MacIntosh et al., 2012). Host and parasite populations are both aggregated in space and time (Bansal, Grenfell, & Ancel Meyers, 2007). Physical contact is an important component of group structure, especially in highly social species like macaques (MacIntosh et al., 2012). Physical contact in group structure can increase the risk of exposure to pathogenic organisms and living in groups creates variation in levels of susceptibility based on an individual's position within the group (MacIntosh et al., 2012). Individual parasitic load assessments within a group or population can help explain the position of individuals within a group, as well as clarify details in group structures. In a population of over 1000 macaques with 5 "super-groups" present in the park, a population parasite framework could potentially explain group structure more easily than a behavioral assessment. Future research on such a network is recommended.

Ecotourism and religious forests create special environments for alloprimates and humans. As forest sizes and alloprimate population sizes have declined, researchers have focused more on the importance of environmental relationships (Dore et al., 2017; Hussain et al., 2013). As resources disappear and more alloprimates come face-to-face with humans, their populations have only become more decimated as humans now begin to see them as pests (Dore et al., 2017). In some instances, alloprimates become immune from the physical attack of people if they reside within a religious area, such as a monkey temple or forest (Dore et al., 2017). The alloprimates often become habituated to human and tourist presence, and some see this habituation as a positive outcome because it theoretically reduces stress and allows the animal to disregard human presence (Walker, Boersman, & Wingfield, 2006). Consequences lie within habituation, especially in areas with high human presence and activity. At sites, including ones similar to Don Chao Poo, habituation results in close contact with humans, which is frequently accompanied by the provisioning of alloprimates with unnatural foods (Loudon et al., 2006). Additionally, close contact with alloprimates and humans has been known to increase rates of disease transmission in naïve populations (Graczyk et al., 2002, Köndgen et al., 2008). Alloprimates are our closest biological relatives and due to our evolutionary attachment, we hold a unique and special relationship with each other both biologically and socially.

Conclusions

I found that long-tailed macaque mother and infants living in a free-ranging population within a monkey forest showed some group level differences in behavior, parasite load, and body condition. I believe that the observed differences within the small sample size is indicative of greater population parasite loads. The parasite load of the 40 sampled mother and infants showed variability between both age class and groups. Variation within and between groups is unclear but is most likely influenced by human activity, anthropogenic foods, age of the individual, space constraints, and location of the group within the park. Although, the gate group, who had the most human approaches recorded, had the lowest parasite load. This study supports previous research that M. fascicularis with higher anthropogenic contact have fewer parasites in adulthood than those with less human contact (Lane et al., 2011)

Behavioral differences were most notable within the middle group, since all significantly different state behaviors were associated with the middle group, suggesting that the mothers of the middle group interact with their infants in a comparatively unique way. Differences in the number of human approaches did not clearly distinguish the behavioral variation see in the mothers of the four groups. Infant behavioral differences are most likely attributed to age differences and resource availability, although maternal behaviors strongly influence infant behaviors as well. The differences in behavior between the four groups is difficult to explain, and is likely a consequence of various factors including, human activity, group size, resource availability, and space constraints.

The original goal of this project was to understand how behavior was influenced by parasite load. Behavior and parasite load were unable to be correlated in this study due to sampling challenges, but I postulate that the pathology of parasites is likely to affect the behavior of certain individuals. No relationship was found between body condition scores and parasite load. Body condition scores were greatest in the middle group, suggesting they eat more unnatural foods (Loudon et al., 2006). The middle group mothers had the lowest parasite count, and the second highest rate of human approaches. The middle group might have developed a greater immunity to parasites due to their high contact rate from humans and consumption of unnatural foods. The pond group had the lowest body condition scores, but highest parasite diversity, suggesting that their body conditions could be influenced by different food resources, group size, or other unquantifiable life history variables.

Future directions

Don Chao Poo forest in Phana, Thailand is a distinctive forest and deserves more attention in research. The monkeys of Don Chao Poo forest not only battle human parasite transmission, but also transmission from domestic animals due to their close proximity to human residences and farms. Park caretakers note that dogs frequently threaten the macaques and sometimes attack them. Future research should address the specific nature of the human-alloprimate relationship in this religious setting. Religious parks and temples where alloprimates are culturally protected creates a unique pathogenic setting and allows us to ask ourselves should we be visiting and interacting with these settings if we have no religious connection to them? Is the additional presence of tourism more harmful and what zoonosis could be acquired by visitations? Not only do researchers need to increase focus on human impact, but the by-products of anthropogenic presence as well, such as the threat of domesticated animals towards wildlife. What is the unique ecological-alloprimate relationship? How can we assess human impact on the forest and monkeys? How does the bi-directional relationship between the health of humans and alloprimates function and what are its larger implications? Should tourists be visiting religious sites, especially ones that are not equipped or used to high rates of visitation? These questions could help contextualize the health of macaques in this forest.

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APPENDIXES

APPENDIX A – *Macaca* Diversity

Table A1
Macaca Diversity

Common Name	**Linnean Name**	**Location**
Stumptailed macaque	*M. arctoides*	Bangladesh, Burma, Cambodia, SW China, India, Laos, Malaysia, Thailand
Eastern Assamese macaque	*M. assamensis assamensis*	Burma, China, India, Laos, Thailand, Vietnam, Bhutan
Western Assamese macaque	*M. assamensis pelops*	Bhutan, India, Nepal
Taiwan macaque	*M. cyclopis*	Taiwan
Common long-tailed macaque	*M. fascicularis fascicularis*	Indonesia, Kalimantan, Sumatra, Lesser Sunda Islands, Brunei, Cambodia, Laos, Malaysia, Philippines, Thailand, Vietnam
Dark-crowned long-tailed macaque	*M. fascicularis atriceps*	Thailand

Table A1 (Continued)

Common Name	**Linnean Name**	**Location**
Burmese long-tailed macaque	*M. fascicularis aurea*	Bangladesh, Burma, Thailand
Con son long-tailed macaque	*M. fascicularis condorensis*	Vietnam
Simuelue long-tailed macaque	*M. fascicularis fusca*	Indonesia
Karimunjawa long-tailed macaque	*M. fascicularis karimondjawae*	Indonesia
Lasia long-tailed macaque	*M. fascicularis lasiae*	Indonesia
Philippine long-tailed macaque	*M. fascicularis philippinensis*	Philippines
Maratua long-tailed macaque	*M. fascicularis tua*	Indonesia
Nicobar long-tailed macaque	*M. fascicularis umbrosa*	India
Japanese macaque	*M. fuscata fuscata*	Japan
Yaku macaque	*M. fuscata yakui*	Japan
Heck's macaque	*M. hecki*	Indonesia
Northern pigtail macaque	*M. leonina*	Bangladesh, Burma, Cambodia, China, India, Laos, Thailand, Vietnam

Table A1 (Continued)

Common Name	**Linnean Name**	**Location**
Moor macaque	*M. maurus*	Indonesia
Indian rhesus macaque	*M. mulatta mulatta*	Afghanistan, Bangladesh, Bhutan, India, Nepal, Pakistan
West Chinese Rhesus macaque	*M. mulatta lasiota*	China
South Chinese rhesus macaque	*M. mulatta littoralis*	China
Moor macaque	*M. maurus*	Indonesia
Indian rhesus macaque	*M. mulatta mulatta*	Afghanistan, Bangladesh, Bhutan, India, Nepal, Pakistan
West Chinese Rhesus macaque	*M. mulatta lasiota*	China
South Chinese rhesus macaque	*M. mulatta littoralis*	China
Insular Chinese rhesus macaque	*M. mulatta sactijohannis*	China

Table A1 (Continued)

Common Name	**Linnean Name**	**Location**
Indochinese rhesus macaque	*M. mulatta siamica*	Burma, China, Laos, Thailand, Vietnam
North Chinese rhesus macaque	*M. mulatta tcheliensis*	China
Tibetan rhesus macaque	*M. mulatta vestita*	China
Sundaland Pig-tailed macaque	*M. nemestrina*	Indonesia, Malaysia, Thailand
Crested black macaque	*M. nigra*	Indonesia
Dumoga-Bone macaque	*M. nigrescens*	Indonesia
Booted macaque	*M. ochreata*	Indonesia
Muna-Butung macaque	*M. orchreata brunnescens*	Indonesia
Pagai macaque	*M. pagensis pagensis*	Indonesia
Siberut macaque	*M. pagensis siberu*	Indonesia
Dark-bellied bonnet macaque	*M. radiata radiata*	India
Pale-bellied bonnet macaque	*M. radiata diluta*	India

Table A1 (Continued)

Common Name	**Linnean Name**	**Location**
Lion-tailed macaque	*M. silenus*	India
Common toque macaque	*M. sinica sinica*	Sri Lanka
Pale-fronted toque macaque	*M. sinica aurifrons*	Sri Lanka
Tibetan macaque	*M. thibetana*	China
Tonkean macaque	*M. tonkeana*	Indonesia

APPENDIX B – *Macaca* Habitat

Table B1

Reported Habitat Types Inhabited by Long-tailed Macaques

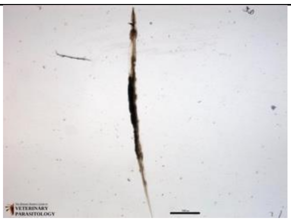
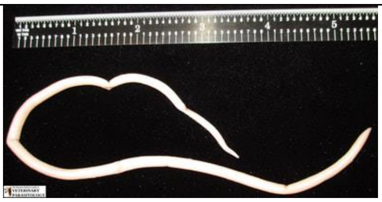
Bamboo forest
Beach
Broadleaf forest
Coastal regions
Deciduous forest
Dipterocarp forest
Dry forest
Edge habitats
Evergreen forest
Grassland
Hills
Islands
Lowland forest
Mangrove forest
Mixed forest
Montane forest
Primary forest
Rain forest
Riverine
Rocky shores
Scrub forest
Secondary forest
Semideciduous forest
Submontane forest
Swamp forest
Tropical forest

Citations: (Chih Mun Sha & Hanya, 2013; Gumert, 2011)

APPENDIX C - Parasites

Table C1

Five Common Parasites Found in Primate Species

Parasite	Egg	Adult
Trichostrongylus sp.	 	
Strongyloides sp.		
Oesophagostomum sp.		
Enterobius sp.		
Ascaris sp.		

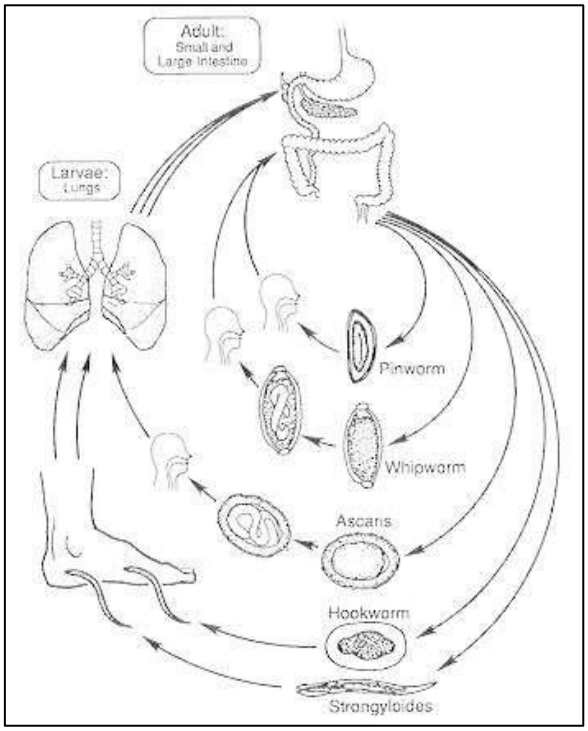


*Figure C1***.** Generalized life cycle of intestinal nematodes

Source: Medical Microbiology. 4th edition. Baron, S. 1996.

APPENDIX D – Parasite Figures

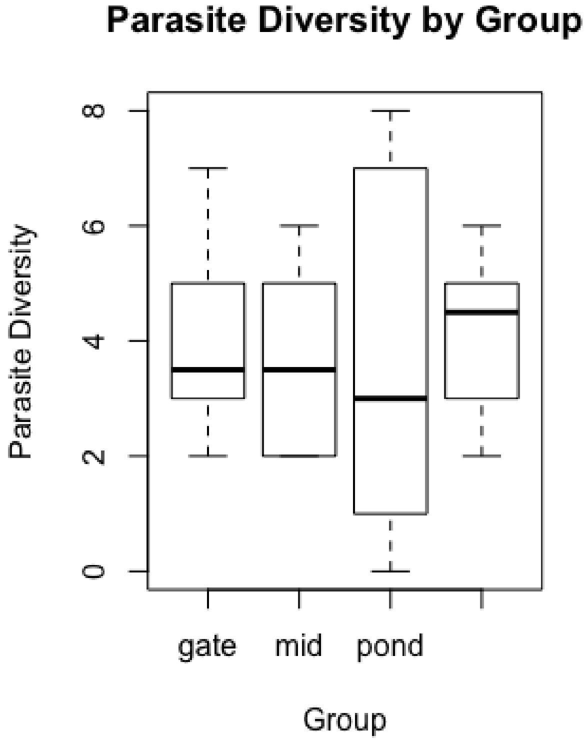


Figure D1. Mother and infant parasite diversity per group

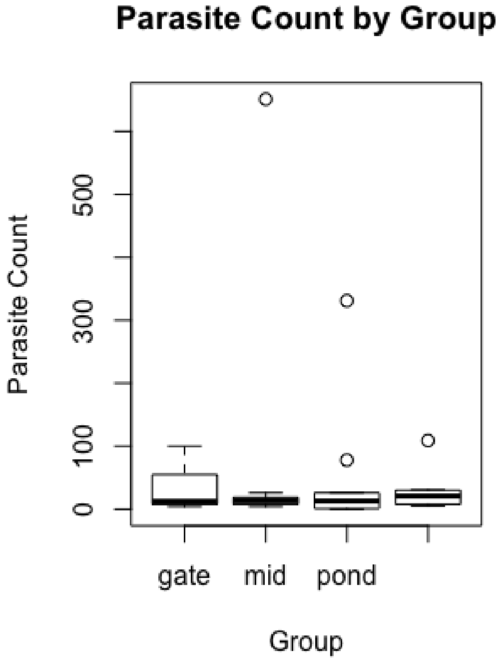


Figure D2. Mother and infant parasite count per group

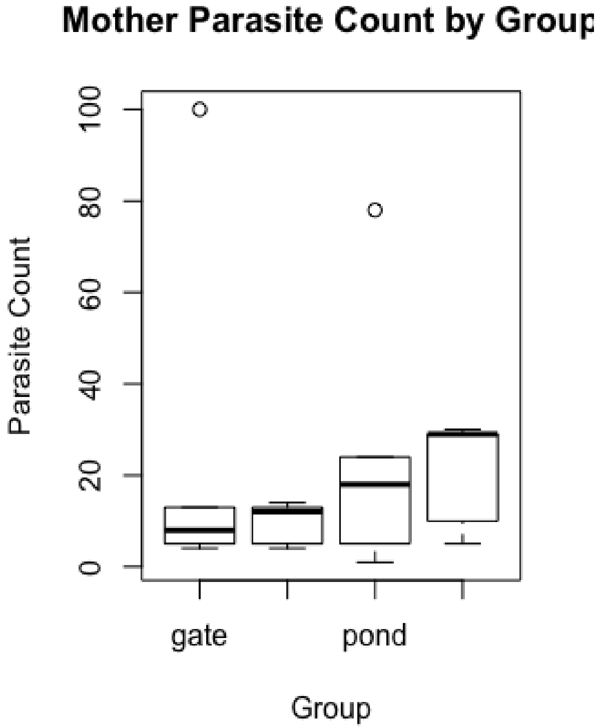


Figure D3. Mother parasite count per group

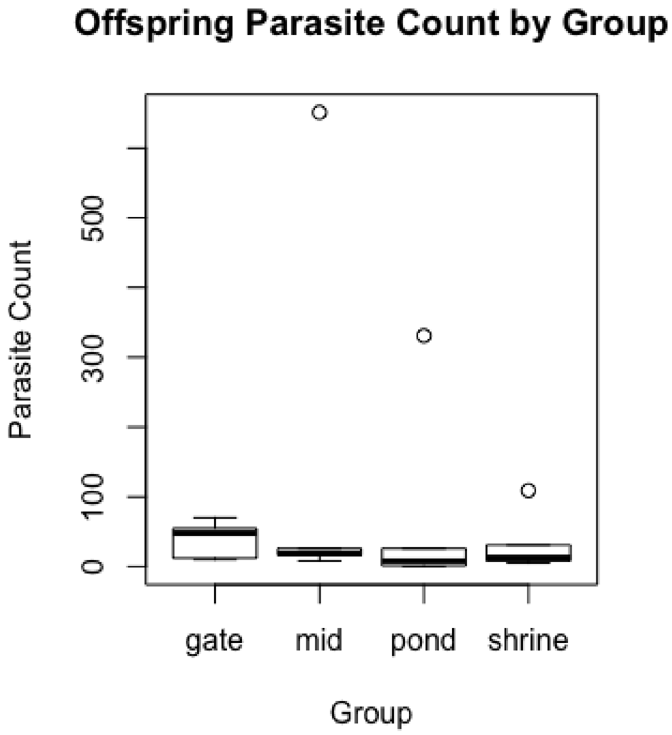


Figure D4. Infant parasite count per group

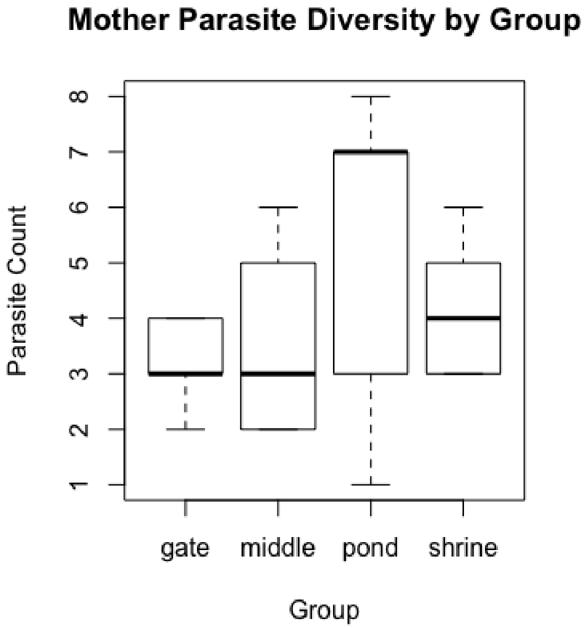


Figure D5. Mother parasite diversity per group

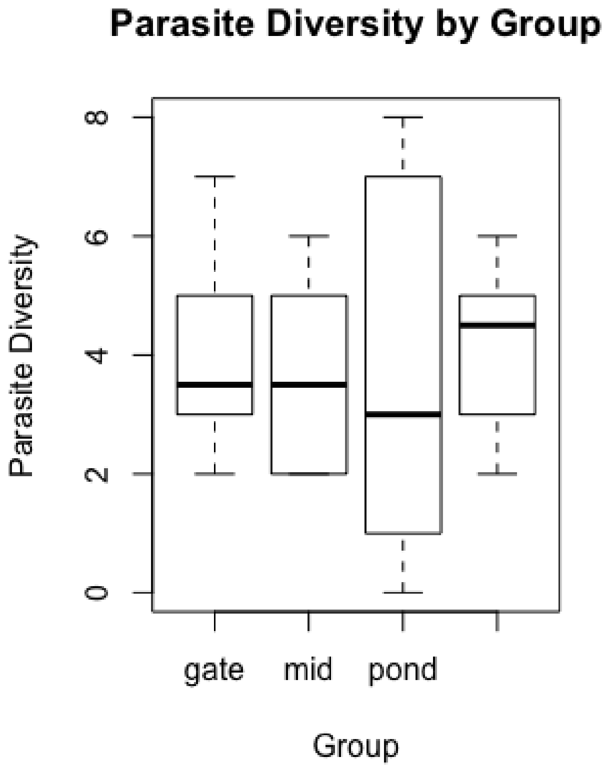


Figure D6. Infant parasite diversity by group