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Ethnoprimatology and Nature-Based Tourism: An Exploration of Macaque Ecology and Behaviour at the Sepilok Orang-utan Rehabilitation Center in Sabah, Malaysia

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A thesis submitted in partial fulfillment of the requirements for the Doctor of Philosophy degree in Anthropology

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Abstract

A rise in tourism revenue worldwide has included an increase in the number of travellers seeking experiences with the natural world. Commonly referred to as *ecotourists*, these visitors typically hail from Western countries and favour locations that allow them to connect with nature in ways they consider sustainable and ethical. However well-meaning, these ecotourist ventures are complex because, while tourism revenue may help protect fragile ecosystems, an increase in tourists can threaten local flora and fauna through increased foot traffic, noise, pollution, and infectious diseases.

Primates are a salient example of this double-edged sword because they are a popular attraction among travellers, meaning they may benefit from increased habitat protection while being at risk from anthropogenic disturbances. The aim of this project was to explore some of the impacts of ecotourism on a wild group of hybrid macaques (*Macaca fascicularis* x *M. nemestrina*) that live alongside two wildlife rehabilitation centers in Sepilok, Malaysia. I used several methodological approaches to assess the experiences and perceptions of visitors to the centers, as well as the impact of tourists on macaque aggression and feeding and ranging behaviour. I also measured the parasite species richness and prevalence of helminths from faecal samples collected during full-day follows.

Most visitors to Sepilok were motivated by a desire to see orang-utans and were largely unaware of the risks of disease transmission. Visitor-directed aggression from macaques was less frequent and less intense when compared to other tourist sites throughout Asia. The macaques frequently fed on provisions intended for the rehabilitating wildlife and rested more after doing so. The group tended to avoid the tourist area during peak visiting hours but still spent a considerable amount of time in close proximity to

visitors. Parasite species richness among the macaques appeared low compared to other sites.

This research highlights some of the complications associated with nature-based tourism that is intended to support conservation. Curtailing undesirable tourist behaviour is difficult, but these results demonstrate that successful education and staff supervision can have tangible effects on primate well-being by reducing direct contact with humans while also providing supplemental nutrition that may bolster immune function.

Keywords

Ethnoprimateology, Tourism, Human-Wildlife Interactions, Macaques, Biological Anthropology, Disease

Summary for Lay Audience

Although tourism programs can help conserve areas that are at risk for development, it can also cause problems by exposing wild animals and fragile ecosystems to human activity. Visitors may unknowingly cause damage to plants by straying from the path, or their physical presence might disrupt nearby animals. Perhaps most importantly, people are capable of sharing diseases with wild animals. Primates are especially vulnerable to this threat because they are so closely related to us and can die after becoming infected with human diseases.

Many tourists are unaware of these risks and seek experiences with primates throughout the tropics. This means that it is crucial for researchers to understand how visitors might disrupt the normal behaviour of wild primates. I wanted to help address this issue by studying a group of wild macaques that live near a popular tourist destination in Sabah, Malaysia. People come from all over the world to visit the Sepilok Orang-utan Rehabilitation Center and the Bornean Sun Bear Conservation Center, which take in orphaned and injured animals with the hope of someday returning them to the wild.

I studied the macaques and tourists at Sepilok in order to understand how tourist beliefs and behaviour affect the well-being of the macaques. People were not allowed to feed the animals, which meant that the macaques were rarely aggressive towards tourists. The macaques avoided the tourist area slightly during the busiest parts of the day, but they still spent a lot of their time near people without taking much notice of them. The group was frequently observed taking fruit and vegetables from the orang-utans and sun bears, and they tended to rest more on days when they did so. This easy access to food may explain why the group had fewer intestinal parasites compared to other monkeys across

Asia, but more research is needed to know for sure. These results will help both researchers and rehabilitation center staff identify the effects of tourists on wild primates with the hope of developing education programs to limit the negative effects of tourism on both people and wildlife.

Co-Authorship Statement

Chapters 3,4, 5, and 6 are co-authored by Dr. Ian Colquhoun, who contributed to the project design, data analysis, and write-up.

Chapter 4 was also co-authored by Dr. Sympharosa Sipangkui, who secured the government permission necessary to complete this research.

Chapter 5 was also co-authored by Richard Burger, who assisted with spatial and statistical analysis.

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List of Acronyms

BSBCC – Bornean Sun Bear Conservation Center

CPG – cysts per gram of faeces

GCM – grid cell method

EPG – eggs per gram of faeces

ETT – epidemiological transition theory

KUD – kernel utilization distribution

LTM – long-tailed macaque

MCP – minimum convex polygon

PSR – parasite species richness

PTM – pig-tailed macaque

SORC – Sepilok Orang-utan Rehabilitation Center

Chapter One

1 Introduction

1.1 *Statement of the Problem*

The potential for tourism to contribute to conservation efforts is based on the premise that sustainable, well-managed programs can employ local residents, educate visitors, and provide funding for the preservation of fragile ecosystems (Honey, 2008). However, this nature-based approach is predicated on the ability to anticipate and manage tourist behaviour in order to reduce their negative impacts on local flora and fauna. Regardless of the intentions of staff or visitors, wild primates are particularly susceptible to negative outcomes following exposure to humans and their pathogens (Wallis & Lee, 1999).

Community-managed programs that focus on nature-based tourism may also be difficult to implement because of the inherent power structures associated with access to the financial capital necessary to develop and maintain facilities that are acceptable to predominantly Western visitors (Chambers, 2010; Fletcher, 2015).

The tourism industry is tied to an increasingly global economy, where easy access to air travel has made long-haul flights more accessible, while changes in land use, expanding cash crops, and fluctuating climatic conditions render food and income security more precarious (Campbell et al., 2016; Green, Hagen, & Mulvaney, 2016; Hoogendoorn & Fritchett, 2016). Understanding the effects of tourism on primate populations must be done in consideration of the multitude of social factors that influence the desire of tourists to explore nature, as well as the financial and ideological incentives for local stakeholders to participate in tourism initiatives.

The overall aim of this research is to explore the interactions between wild macaques (*Macaca* spp.) and tourists in an environment where visitor behaviour is restricted by rules that are enforced by staff members at an adjacent pair of wildlife rehabilitation centers (see below). I also sought to understand how tourists' understanding of infectious disease risk and conservation issues affected their behaviour when close to the wild primates. In doing so, this work contributes to the growing body of knowledge on the risks of wildlife tourism, socioecological entanglements between primates and local communities, and the various attempts to curb unwanted tourist behaviour for the sake of the well-being of wild primates. The study of primate tourism is complex because it involves considerable risk to the health of both humans and non-human primates as well as a confluence of behavioural, economic, genetic, epidemiological, ecological, and physiological factors, many of which are beyond the scope of this dissertation. My research addresses some of these components by answering the following research questions:

- 1) What perceptions do tourists have regarding primates, local conservation issues, and infectious disease?
- 2) Does tourist behaviour affect the likelihood of experiencing human-directed aggression from macaques?
- 3) How does proximity to a tourist site and related provisioning behaviour affect the feeding and ranging patterns of wild macaques?
- 4) What helminth genera are present in a mixed-species group of macaques?

Research that takes a multi-species approach to infectious disease in both humans and animals has become crucial in light of the increase in zoonoses and anthroozoonoses

worldwide. Known as the *One Health* approach, interdisciplinary methods to monitor disease patterns have called for an integration of human, animal, and plant health due to the cumulative effect of environmental conditions on the emergence and spread of disease (Destoumieux-Garzón et al., 2018). Ethnoprimatological research falls within the One Health paradigm because it highlights the confluence of biological, social, and economic influences on human-primate and disease transmission (Fuentes & Hockings, 2010). Projects such as this one that attempt to identify effective tourist management strategies are an essential component in the on-going effort to mitigate the potential threats of tourism to wild primate populations.

1.2 Study Site

The study group featured in this research consisted of long-tailed macaques (*M. fascicularis*), pig-tailed macaques (*M. nemestrina*), and their suspected hybrid offspring. As the only macaque group that visits the Sepilok Orang-utan (*Pongo pygmaeus*) Rehabilitation Center and the Bornean Sun Bear (*Helarctos malayanus*) Conservation Center regularly, they represent a unique opportunity to study the behaviour of macaques that encounter tourists frequently while benefitting from staff-managed provisions that are intended for the rehabilitating animals (Figure 1.1).

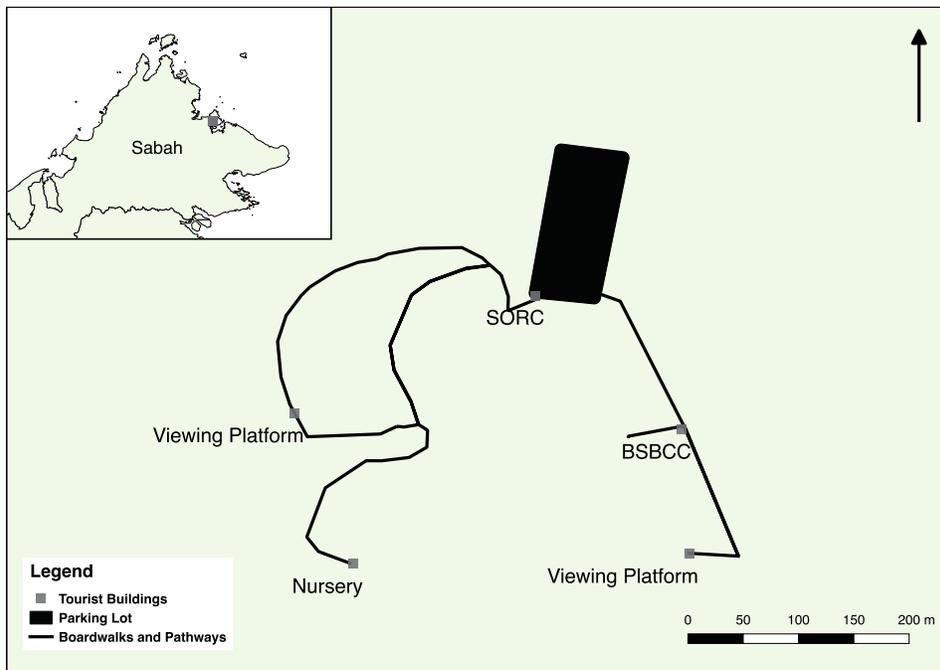


FIGURE 1.1. Map of the Sepilok Orang-utan Rehabilitation Center (SORC) and the Bornean Sun Bear Conservation Center (BSBCC).

1.3 Thesis Organization

Chapter two connects the multiple subdisciplines that are relevant to an ethnoprimateological approach to tourism and primate health. The history of infectious disease, biotic and abiotic factors among both humans and primates, emerging trends in tourism and land use patterns, as well as the ever-increasing threat of climate change all contribute to the multifaceted patterns in disease transmission between humans and animals (Chambers, 2010; May 1958; Patz et al., 2004; Wallis & Lee 1999). The literature review introduces these concepts and their relation to nature-based tourism.

Chapter three outlines the experiences, perceptions, and motivations of visitors to the Sepilok Orang-utan Rehabilitation Center and the Bornean Sun Bear Conservation Center. Semi-structured interview data provide insight into the drivers of undesirable tourist

behaviour, such as close proximity to orang-utans, while situating rehabilitation centers within the broader conservation context of sustainable wildlife tourism.

Chapter four explores the rates and intensity of macaque aggression towards visitors at Sepilok. Since visitor behaviour is likely to influence rates of aggression, it is important to assess patterns in both visitor and macaque behaviour. The distribution of aggressive behaviour throughout the macaque group is discussed along with a comparison to similar studies on rates of contact with tourists throughout Asia.

Chapter five summarizes feeding and ranging data of the focal macaque group. Also discussed are the potential concomitant effects of the macaque group's feeding and ranging behaviour on parasite exposure as well as morbidity and mortality patterns in wild primates that feed on provisioned food near tourist sites.

Chapter six provides a glimpse into the parasite prevalence of the study group while outlining potential future research questions that can build on this preliminary study. Many of the logistical issues that plague non-invasive parasite research are discussed in the hopes that it will better inform future researchers.

Chapter seven summarizes the relevance of the current study to the broader body of literature on primatology, tourism, and infectious disease. A number of potential future lines of inquiry are identified.

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Chapter Two

2 Literature Review

2.1 Introduction

There are a number of theoretical paradigms that underpin research on primates, disease transmission, and tourism. In a seminal work on the ecology of disease, May (1958) argued that pathogens are involved in a complex network of relationships both within and between hosts, and it is therefore prudent to study infectious disease from both a social and biological perspective. The purpose of this chapter is to outline the multiple scholarly influences that have contributed to a combined biocultural approach to tourism and disease. I start with a brief introduction into the theory of infectious disease and expand by contextualizing zoonotic and anthrozoonotic disease within the Order Primates using both evolutionary medicine and the epidemiologic transition theory. Both the theory of infectious disease and evolutionary medicine are important tools in understanding the significance of tourism as a source of emerging public health and conservation risks. I weigh the costs and benefits of tourism as a source of conservation revenue and as a deterrent for illegal activity, which introduces the holistic ethnoprimateological paradigm as a way of understanding interactions between both human and non-human primates.

2.2 Theoretical Paradigms

2.2.1 Infectious Disease

There are numerous and complex conditions necessary for new infectious diseases to emerge and thrive within an ecological niche. For the purposes of this chapter, we can

summarize the theory of infectious disease in primates in three postulates: 1) the more closely related two primates species are, the more likely it may be that any given pathogen will travel between them (Davies & Pedersen, 2008; Cooper, Griffin, Franz, Omotayo, & Nunn, 2012; Fountain-Jones et al., 2018); 2) cross-species transmission may occur when pathogens are encountered in infected bodily excretions, vectors, or on inanimate surfaces (Jones-Engel et al., 2005); and 3) human behaviour drives disease transmission by facilitating close contact with primates (Wallis & Lee, 1999; Weber, Alroy, & Scheiner, 2017). Therefore, humans may affect morbidity and mortality in primates in two ways: biologically, by directly or indirectly introducing new pathogens to a population; and socially, by affecting primates' exposure to other animals or environmental helminths via inflated feeding competition and altered ranging patterns and substrate use (Berman, Li, Ogawa, Ionica & Yin, 2007; Muehlenbein & Wallis, 2014; Nunn, Altizer, Jones, & Sechrest, 2003; Sponsel, 1997; Woodford, Butynski, & Karesh, 2002). These biological and social factors are inextricably linked, which makes an anthropological approach an ideal tool to investigate disease patterns in wild primates in a tourism context because of the human influence on primate behaviour and ecology.

2.2.2 The Biocultural Approach and Evolutionary Medicine

Anthropologists are well positioned to investigate changes in emerging infectious disease (EID) patterns using evolutionary, ethnographic, and archaeological lines of evidence. A holistic anthropological approach devoid of sub-disciplinary boundaries is essential because EID is at once both cultural and biological (Inhorn & Brown, 1990). The frequent combination of biological and cultural lenses to address human health and evolution led to

the rise of the *biocultural* approach in anthropology, which focuses on the “dynamic, dialectical interactions between humans and their larger physical, cultural, and social environments” (Zuckerman & Martin, 2016:7). While there is no single theoretical paradigm associated with biocultural research, most modern discussions of a biocultural approach in anthropology continue to measure the effects of social factors on one or more aspects of human biology (Wiley & Cullin, 2016). The term ‘biocultural’ did not appear until the 1970s, but its conceptual origins date back to at least the 1950s. Early biocultural research by Livingstone (1958), for example, helped establish a relationship between human subsistence strategies, mosquito ecology, and a selection for the sickle cell gene in West Africa where malaria was most prevalent.

The study of evolutionary medicine is also related to biocultural research insofar as it explores the proximate causes and ultimate treatments of health-related issues by questioning how variation in human behaviour, morphology, and physiology affect susceptibility to disease (Muehlenbein, 2013). The evolutionary medicine paradigm is based on the argument that large-scale evolutionary processes can help us to better understand disease patterns by elucidating pathogen, vector, and host life histories (Mercer, 2018). Disease transmission between humans and non-human primates is an excellent example of this, where both social behaviour and biology can have measurable effects on morbidity and mortality.

May (1958) helped establish an evolutionary approach to the study of the ecology of human disease by situating disease as the result of inorganic, organic, and sociocultural stimuli combined with the subsequent tissue response. Inorganic conditions such as wind, heat, and trace elements found within soil can affect pathogen and vector growth and

spread, while also impacting human health. Meanwhile, organic stimuli comprise the ecological niches where pathogens, vectors, and hosts interact. Synecological relationships between species may become altered as inorganic stimuli change over time, which can allow for a shift in disease prevalence (May, 1958). For example, fluctuations in inorganic stimuli, such as temperature, rainfall, and/or soil composition may facilitate an increase in helminth reproduction, resulting in higher rates of morbidity among primates.

Both May (1958) and Livingstone (1958) recognized that biology alone is not sufficient to shape epidemiological patterns. Social and cultural patterns can affect infectious diseases either positively or negatively. For example, humans may encourage mosquito proliferation by allowing pools of standing water to accumulate. However, cultural adaptations such as the use of mosquito nets and biomedical advancements can simultaneously limit the morbidity and mortality rate of infectious vector-borne diseases. The term ‘biocultural’, then, includes the confluence of complex ecological systems, external climatic factors, and organism behaviour; all of which exist in a reciprocal relationship where they influence one another (May, 1958). Despite the fact that May and Livingstone published their landmark research more than sixty years ago, their work continues to inform interdisciplinary investigations of disease (e.g. Barrett & Armelagos, 2013; Brewis, 2010; van Gerven, Carlson, & Armelagos, 1973).

Disease patterns in primates are the result of the external climate (inorganic stimuli), the shared ecological niche between primate species (organic stimuli), and the social behaviour of both primates and humans (sociocultural stimuli). This project attempts to address all three of these components by exploring the ecology, behaviour, and parasite prevalence of macaques that share a significant part of their home range with humans.

2.2.3 Epidemiologic Transition Theory

Research that relied on a holistic approach to infectious disease during the second half of the 20th century helped to contextualize the epidemiologic transition theory (ETT), which posits that shifts in disease prevalence and mortality patterns are a consequence of changes in human demography, social behaviour, and technology. In his formative work on human epidemiology, Omran (1971) describes three different epidemiologic transitions where large scale changes in patterns of human disease occurred at the population level. The first wave of the epidemiologic transitions began following the large-scale transition to sedentary agricultural societies approximately 10,000 years ago (Barrett, Kuzawa, McDade, & Armelagos, 1998). Prior to this change, isolated and nomadic communities would have been largely free of acute respiratory diseases and viruses including measles, mumps, and small pox (Armelagos, Brown, & Turner, 2005; Barrett et al., 1998). Conversely, pathogens with reduced virulence or with extended periods of latency would have had more success in infecting nomadic groups; chicken pox and herpes may have been sustained despite low rates of contact between populations (Barrett et al., 1998). Not unlike today, pre-agricultural communities would have been exposed to parasites while locating, preparing, and consuming uncooked plants and animals (Barrett et al., 1998). However, zoonoses contracted in this manner would likely have seriously affected only a small number of individuals within a group before disappearing (Armelagos et al., 2005). The small population size and high mobility of gatherer-hunters would have made diseases for which humans were the only host particularly unlikely to thrive (Barrett et al., 1998; Cockburn, 1971).

The epidemiology of infectious disease changed rapidly as human populations began to trade nomadic hunting and gathering for sedentism and large-scale food production. With the increased reliance on animal domestication, the transmission of zoonotic pathogens, such as brucellosis or anthrax, became more likely (Polgar, 1964). Thus, the first wave of the ETT, the Age of Pestilence and Famine, featured high mortality rates, a low and fluctuating life expectancy, and a lack of sustained population growth. Malnutrition, disease, and infection affected children and women of child-bearing age most significantly (Omran, 1971).

The second wave, known as the Age of Receding Pandemics, began at approximately 1650 CE in western Europe and saw a steady decline in mortality rates, allowing for an increase in life expectancy at birth and the beginning of an exponential rise in population growth. Improvements in hygiene and nutrition generally allowed for a sharp decrease in the mortality rate of adult women due to improved survival rates during childbirth, creating a more equal sex distribution amongst adults (Omran, 1971). Despite the decline in overall mortality, infectious diseases such as tuberculosis, typhoid, and dysentery still caused the greatest number of deaths (Mercer, 2018).

According to Omran (1971), societies in the developed world are now typically considered to be in the third wave of the epidemiologic transition: The Age of Degenerative and Man-made Diseases, where pestilence, famine, and epidemics have been replaced by a drastic increase in the prevalence of chronic degenerative diseases, (e.g. heart disease) and diseases of lifestyle (e.g. type II diabetes) (Worthman & Kohrt, 2005). An important caveat in discussing the ETT is that not all populations will make the same transition at the same time, nor at the same pace (Omran, 1971). There are significant differences in morbidity

and mortality between socio-economic classes, race, sex, and across geographic locations (Mercer, 2018; Santosa, Wall, Fottrell, & Högberg, 2014). Therefore, we cannot expect to see homogenous changes across an entire population.

Omran's original theory not only fails to address community level discrepancies in social determinants of health, but it also lacks a discussion of increasingly complex mortality and morbidity patterns in the developed world. More recently, researchers have argued that there are two additional transitions underway: i) the age of declining cerebrovascular mortality, increased longevity, and lifestyle modifications; and ii) the increased importance of emerging, re-emerging, and antibiotic-resistant pathogens such as HIV and multi-drug resistant tuberculosis (Barrett et al., 1998; Mercer, 2018; Omran, 1971). The latter trend is relevant to the current study because sharp increases in severe infectious disease have the potential to slow down or reverse progress in delayed mortality. This is demonstrated by the significant impact of tuberculosis and HIV/AIDS in Philadelphia and South Africa, respectively, where increased mortality occurred irrespective of global trends towards a longer life expectancy (Condran et al., 1982; Kahn, Garenna, Collinson, & Tollman, 2007; Santosa et al., 2014).

In spite of this criticism, the ETT model combined with evolutionary medicine and a biocultural approach remain useful tools in understanding broad trends in infectious disease, particularly in regard to the effects of human behaviour on plant, animal, and microbe ecology. Infectious diseases typically have complex causes and consequences that are well beyond the scope of this dissertation. However, a cursory glance indicates just how many competing factors contribute to the emergence and re-emergence of diseases such as multidrug resistant tuberculosis, Zika virus, influenza, Lyme disease, ebola, and measles

(Ioos et al., 2014; Paules, Marston & Fauci, 2019; Petersen, Bear, & Visser, 2019; Zuckerman, Harper, Barrett, & Armelagos, 2014). Social and biotic factors, such as public health programs (or a lack thereof), deforestation and erosion, antibiotic use, international tourism, wealth disparities, and the rise of pseudoscience influence the biological and cultural conditions that dominate our conversations about disease today (Barrett et al., 1998; Mercer, 2018; Gillespie, Nunn, & Leendertz, 2008; Santosa et al., 2014; Worthman & Korht 2005).

The epidemiologic transition theory allows us to think of disease as a phenomenon that interacts with and responds to human populations; disease patterns shift over time depending on the population, climate, and social conditions. Even when humans are not passing pathogens directly between each other (e.g. Zika, Lyme disease), our aggregate behaviour affects the ecology of both pathogens and their respective insect vectors. The revised ETT model is relevant to discussions of disease and tourism because it uses an anthropological lens to place EID at the intersection of human culture, the environment, and biology (Ewald, 2010; Turshen, 1977). We can expect further refinement of the ETT paradigm over the coming years as the importance of the feedback loops associated with EID are addressed via the One Health approach to disease (Destoumieux-Garzón et al., 2018).

2.2.4 Primate Phylogeny

In addition to biocultural paradigms, an evolutionary medicine approach to EID is important because both emerging and re-emerging diseases are the result of multifaceted interactions between hosts, vectors, and pathogens *vis à vis* social, genetic, and ecological

processes (Wolfe et al., 1998). Primates in general, and tourism in particular, tie together all three of these components. Tourists seek opportunities to observe and interact closely with non-human primates, which provides local stakeholders with financial benefits. Meanwhile, the close phylogenetic relationships between primate species make pathogen sharing possible to begin with (Zuckerman et al., 2014). Given that the likelihood of disease crossover increases as phylogenetic distance decreases, knowledge of primate phylogeny allows researchers to better anticipate which pathogens are most likely to successfully jump between species (Wolfe et al., 2007). Research into primate host specificity and transmission strategies revealed that at least 114 parasites were documented to be shared between humans and other primates, either through a shared evolutionary origin or zoonotic transmission. Furthermore, upwards of 28% of non-human primate viruses were classified as ‘emerging’ in humans (Pedersen, Altizer, Poss, Cunningham, & Nunn, 2005). Moreover, the propensity for humans to interact with wild non-human primates in multiple different contexts allows for frequent close contact between species, which is an important precursor for novel disease transmission (Inhorn & Brown, 1990; Fenton and Pedersen, 2005; Maréchal, MacLarnon, Majolo, & Semple, 2016; Schillaci et al., 2005; Wolfe et al., 2007). For example, research on the zoonotic malaria parasite *Plasmodium knowlesi*, which uses long-tailed macaques as a natural host, has found that humans who spend more time in working in plantations are at a greater risk for contracting the disease via mosquito vectors (Barber et al., 2012). Such findings have highlighted the fact that not only are pathogens theoretically capable of moving between primate genera due to close phylogenetic relationships, but that such transitions are already causing public health issues in humans.

2.2.5 Parasites in an Ecological Context

The term *parasite* may refer to either ectoparasites that can be found outside of a host's body (e.g. lice) or endoparasites that live inside the host's body (e.g. helminths) (MacIntosh, 2016). Protozoa and helminths can enter a host's body through contaminated food, water, or soil, and they may be either pathogenic or non-pathogenic (Balasubramaniam, Sueur, Huffman, & MacIntosh, 2019). This variability in the severity of helminth infection means that the effect on hosts may range from negligible to severe (Agostini, Vanderhoeven, Di Bitetti, & Beldomenico, 2017).

Although parasites have often been discussed as something unnatural and worthy of eradication, recent shifts towards an evolutionary approach to infectious disease have highlighted the important role that parasites play in their respective ecosystems (Poulin, 2007; Schmid-Hempel, 2011; Muehlenbein, 2013). The emergence of the therapeutic use of microbes to treat modern day inflammatory and autoimmune diseases in humans highlights a distinct shift towards evolutionary medicine; parasites are no longer uniformly regarded as enemies that need to be evicted. Rather, their potential for mutualism, commensalism, or parasitism with their host is becoming more widely discussed (Cooper, 2009; Hopkins, Wojdak, & Belden, 2017; Lorimer, 2017; MacIntosh, 2014; Nelson & May, 2017).

Viewing parasites as a part of a complex ecological system at both the host and population levels allows us to examine their potential detrimental effects on a host's health and reproductive fitness without assuming that parasite infection is inherently indicative of significant illness (Lorimer, 2017; Nguyen et al., 2015). Parasites are part of a dynamic multi-species interface; thus, a thorough exploration of infectious disease patterns requires an understanding of molecular mechanisms, host and parasite ecology, climatic variation,

as well as population dynamics (Cable et al., 2017; Gillespie, 2006; Schmid-Hempel, 2011; Seguel & Gottdenker, 2017). Although most macaque species (*Macaca* spp.) are not typically considered a conservation priority, they represent an important taxon for parasitological research because they are found in myriad habitats and with varying degrees of human intervention. This provides a unique opportunity to look at the ways in which parasite prevalence and richness vary across anthropogenic contexts.

2.2.6 Parasite Ecology

Parasites are equally susceptible to changes in their environment compared other larger bodied taxa, and their behavioural and reproductive patterns will affect where and when they are able to infect potential hosts. Reliance on intermediate hosts introduces further ecological variables that can also impact their transmission rates. This means that understanding infection risk and consequences requires knowledge of multi-species behaviour and ecology, environmental conditions, as well as short- and long-term climate patterns (Dallas, Park, & Drake, 2017; Lane, Holley, Hollocher, & Fuentes, 2011; Loudon & Sauther, 2013; Muehlenbein, Schwartz, & Richard, 2003; Poulin, 2007).

Parasites will differ in their mode of transmission, meaning they will not be equally likely to move between individuals or species within an environment. Combined with host population density, group size, and species-specific behaviour (such as grooming), parasite transmission strategies can explain a significant portion of epidemiological trends in social primates (Kappeler, Cramer, & Nunn, 2015; Nunn, Altizer, Jones, & Sechrest, 2003; Rimbach et al., 2015). Nematodes (i.e. roundworms) typically undergo development outside of the host before being acquired through contaminated substrata. Therefore, they are less likely to be encountered during social behaviour, such as mating or grooming

(MacIntosh et al., 2012; Sarabian & MacIntosh, 2015; Walther, Clayton, & Gregory, 1999). Oxyurids on the other hand (i.e. pinworms), tend to be spread via faecal-oral transmission, and are therefore more likely to be socially transmitted during close contact behaviour, such as roosting (González-Hernández et al., 2014; Gotoh, 2000). Large groups with high modularity (i.e. many subgroups) typically experience lower rates of parasite richness, though well-connected individuals are still capable of causing outbreaks within the group due to their ability to spread pathogens to multiple group members (Griffin & Nunn, 2012). Solitary animals, such as orang-utans, are thus at a reduced risk of experiencing population-level outbreaks (Carne et al., 2014).

Host feeding and ranging behaviour may also impact parasite acquisition due to the likelihood of encountering pathogens in food, water, or contaminated strata within the environment. Invertebrates can act as an intermediate host for some parasites, meaning omnivorous primates may be exposed to a greater number of unique parasite species compared to folivores (Loudon & Sautner, 2013). Terrestrial primates may be more likely to encounter parasites in soil and leaf litter, while more arboreal primates may come into contact with contaminated faeces amongst the tree branches, though likely less frequently (Chapman et al., 2012; Loudon & Sautner, 2013). Body size may also influence an individual's risk for helminth infection, with larger-bodied individuals acting as a bigger 'island' for parasites with more resources and higher encounter rates when compared to smaller-bodied hosts (Kamiya et al., 2014).

Climate (and, by extension, climate change) can have multiple and seemingly contradictory effects on the effects of parasites, intermediate hosts, and definitive hosts. Rainfall, for example, could impede parasite transmission by washing away infected faeces

from tree branches onto the ground (Chapman et al., 2012). However, it might also facilitate the spread of ground-living helminths who thrive in moist soil and high humidity (Taylor, Coop, & Wall, 2016). Increases in ambient temperature could mean increased parasite growth and infectivity, or increased parasite mortality due to desiccation (Cable et al., 2017; Lane et al., 2011; Poulin, 2007). Changes in climate patterns may allow for host range expansion, which could result in parasites moving into new environments, complicating existing disease management strategies (Mwangi, de Figueiredo, & Criscitiello, 2016). Conversely, climatic shifts might make existing territories inhospitable to either parasites or hosts, causing potential population-level decreases in parasite prevalence (Cable et al., 2017). Habitat degradation caused by a combination of anthropogenic and naturally-fluctuating climate patterns could cause chronic physiological stress in primates, making them susceptible to infection (Kaur & Singh, 2009). Alternatively, such changes could reduce both parasite diversity and concomitant infection risk (MacIntosh, 2014).

Any combination of the above scenarios could have important implications for primate well-being because heightened exposure to parasites can result in an increased risk for adverse health effects in wild primates, such as decreased host fertility, retarded growth, and increased rates of morbidity and mortality (Lane et al., 2011; Agostini et al., 2017). Therefore, it is important to understand how both the presence of humans and the effects of anthropogenic land change more broadly can impact parasite avoidance and acquisition behaviour in wild primates, potentially exacerbating parasite-related morbidity (MacIntosh, 2014).

2.2.7 Ecotourism

There are a number of different definitions of ecotourism, but generally speaking, the term refers to “responsible travel to natural areas that conserves the environment, sustains the well-being of the local people, and involves interpretation and education” (TIES, 2015).

Ecotourists are generally understood to be tourists who express an interest in conservation issues, environmental education, and often stay in 'lodges' to experience the environment in a way that is meaningful to them (Mallapur, 2013). These lodges generally purport to minimize the environmental impact of travel, which might involve cooking with local ingredients or using compost toilets to reduce water use. Ecotourism locations frequently use the term ‘sustainable’ to imply that their resources use does not threaten the local environment’s ability to replenish itself (Chambers, 2010; Honey, 2008).

The ability for ecotourism ventures to meet the goals of community involvement, tourist education, and the safeguarding of local environments is unclear. Groups within a community may have different priorities and may not benefit equally from the hassle of hosting tourists, which can limit support for new for expanding ecotourism ventures (Chambers, 2010; Silva & Mosimane, 2017). Assessing the long-term benefits of environmental education on both foreign and local tourists is difficult and the remote and often under-developed nature of many ecotourism locations is precisely what makes sustainable living so difficult. The need for new or expanded roads, increased foot traffic, and an inability to easily dispose of waste may cause undue pressure on a location that is meant to be protected by the very visitors it strains to support (Chambers, 2010). Further criticism of the ecotourism model points to the sizeable impact of international flights on global greenhouse gas emissions, as well as the deeply embedded structural inequalities

that may prevent local communities from benefiting long term (Honey, 2008; Juvan & Dolnicar, 2014). Even the terms ‘ecotourism’ and ‘sustainable’ can be used in vague contexts in order to attract visitors, regardless of the conditions of a site (Stronza, Hunt, & Fitzgerald, 2019).

This paradox extends to effects on wild primates as well. The perceived benefit of ecotourism is that it can conserve valuable habitats and threatened species while providing meaningful and consistent employment for local communities (Honey, 2008; Woodford et al., 2002). However, this is potentially problematic because sustained close contact between humans and primates increases the risk of disease transmission, and relatively benign pathogens in humans, such as rhinoviruses, can cause serious infection or death in novel species (Wallis & Lee, 1999).

Tourism programs have contributed to the increased protection of fragile mountain gorilla (*Gorilla berengei* ssp.) habitats by preventing both poaching and deforestation for livestock grazing, which has contributed to increased population numbers in the wild (Goldsmith, 2014; Muehlenbein et al., 2010). However, these positive outcomes have followed significant mortality events in wild populations, with up to 20% of sudden deaths in mountain gorillas attributed to human respiratory diseases (Goldsmith, 2014). Tourism presents a significant health risk not only because of humans’ close evolutionary relationship with primates, but because tourists are especially likely to be immunosuppressed due any number of related factors such as fatigue, changes in biorhythm and climate, unfamiliar food, or medication (Woodford et al., 2002). Clinical symptoms of infection in tourists may not be obvious due to medication or long incubation times, so relying on visible signs of disease to assess risk is insufficient (Muehlenbein et al., 2010).

Locations that attempt to educate tourists about environmental issues without necessarily prioritizing sustainability or community involvement may be referred to as nature-based tourism by scholars (Chambers, 2010). The complication with this notation lies in the fact that tourists themselves may not be so discerning about the nuanced differences between nature-based tourism and ecotourism. The current study site, Sepilok, occupies such a liminal state, where it is referred to as an ecotourism site or a type of zoo, depending on who is speaking (see chapter 3, this volume).

2.2.8 Macaques as a Study Species

There is a lengthy history of contact between macaques and humans in both traditional and contemporary cultural contexts, which makes them appropriate subjects for emerging infectious disease research because they may be revered or detested depending on the context (Humble & Hill, 2016). Macaques are distributed widely throughout Asia and North Africa and their ability to thrive in numerous habitats, such as urban, rural, and primary forest areas, means that they interact with humans frequently (Schillaci et al., 2005). Long before modern tourism, macaques were sought out in parts of Asia because of their symbolic importance in the Buddhist, Hindu, and Shinto religions (Fuentes, 2012). Because many current Hindu temples double as tourist attractions, they create a unique context where macaques and humans, both foreign and local, interact closely and consistently. This creates a ‘perfect storm’ scenario where the risk of infectious disease transmission is high (Fenton & Pedersen, 2005; Fuentes, 2012). Macaques have the ability to not only infect humans, but also to ferry human pathogens from forest edges to forest interiors, where they

may infect more endangered primate species or lead to host-switching, as has been the case with *Plasmodia* species (Cox-Singh & Singh, 2008).

Although long-tailed and pig-tailed macaques are not yet listed as Endangered, their populations are in decline throughout their range due to hunting and habitat loss (Eudey, 2008; Richardson, Mittermeier, Rylands, & Konstant, 2008). It is important that conservation action plans extend to Least Concern species in order to mitigate their decline before their situation becomes dire (Eudey, 2008; Malaivijitnond & Hamard, 2008). The bold and flexible nature of these macaques, their sheer population numbers, and their propensity to inhabit edge habitats makes them a likely candidate for affecting both zoonotic and anthrozoonotic disease transmission. This makes the investigation of tourism sites that feature macaques all the more relevant because limiting contact between visitors and animals is an important part of reducing the risk of injury or disease transmission.

2.2.9 Ethnoprimateology

The field of ethnoprimateology has also heavily influenced my approach to the study of tourism and infectious disease in primates. Coined by Sponsel (1997), an ethnoprimateological approach typically focuses on the interface between humans and primates and views all primate species as legitimate participants in both cultural and ecological relationships while highlighting the millennia-long entanglement that has existed throughout primate ranges (Fuentes, 2010; Riley, Fuentes, & Dore, 2017; Sponsel, 1997). Ethnoprimateology rejects the notion of pristine primate groups that are untainted by human influence. Rather, ethnoprimateologists have used multispecies approaches and a diverse

methodological toolkit to answer questions relating to primate and human ecology, predator/prey dynamics, and religious and cultural significance without assuming that contact between humans and primates is inherently unnatural (Lee & Priston, 2005; Sponsel, Ruttanadakul & Natadecha-Sponsel, 2002; Riley, Fuentes, & Dore, 2017). Ethnoprimateology complements biocultural approaches to infectious disease research because both climate change and human land use patterns affect the economic, social, ecological, historical, and epidemiological entanglements between humans and the surrounding wildlife (Fuentes, 2010; Muehlenbein, 2017). The holism of ethnoprimateology also bolsters evolutionary medicine because both biological and cultural factors are highlighted in the emergence and spread of infectious disease.

By rejecting discrete land type categories, such as ‘natural’ versus ‘disturbed,’ ethnoprimateology contributes to a critical review of the ecotourism industry, which typically frames ‘nature’ as a location that people can escape to (Chambers, 2010; Malone et al., 2014; West & Carrier, 2004). An ethnoprimateological approach allows researchers to explore both quantitative and qualitative data, both of which permeate the tourism industry where rates of contact between people and animals can be counted easily, but value-based topics such as conservation priorities are more difficult to describe (Malone et al., 2014). Ethnoprimateology embraces this complexity rather than attempting to narrow the research focus to a more limited methodological approach.

The multifaceted evolutionary relationship between primates combined with humans’ propensity to seek out non-human primates for both livelihood and leisure has created an ecological niche where conflict is likely *if* proactive measures are not taken to reduce risks. My research uses an ethnoprimateological and biocultural approach by addressing the

potential for human influence to act as a driver of non-human primate behaviour and, by extension, overall well-being.

2.2.10 Non-invasive sampling

Over the past few decades there has been a shift in biological anthropology towards the use of non-invasive, non-destructive methods of data acquisition, particularly with respect to the analysis of ancestors' human remains and wild primate populations (Aufderheide, 2003; Strier, 2013). Ethical considerations for this change include the accommodation of descendants' wishes and the potential adverse health effects of capture and sample collection from wild primates. In primatology, specifically, field, captive, and laboratory studies have all used different methods of invasive sampling to collect saliva, blood, faeces, semen, and cerebra-spinal fluid for analysis. Invasive sampling can yield high quality samples in sufficient quantity for analysis. However, it typically requires a combination of physical restraint, anesthesia, potentially complex sampling procedures, recovery time, and release. All of these components put the primate at risk of injury or death, and close contact between humans and potentially aggressive primates (as well as the presence of sharp objects such as syringes and metal cages) increases the risk of both zoonotic and anthrozoonotic disease transmission (Simons et al., 2012). Thus, invasive sampling has been argued to be both impractical and unethical in field primatology (Kawai et al., 2014).

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Chapter Three

3 “There’s Bloody Monkeys Everywhere!”: Visitor Motivations and Perceptions of Primates

3.1 *Introduction*

3.1.1 *Ecotourism*

Research on nature-based sustainable tourism (also known as ecotourism) has grown exponentially in the past 30 years (Ruhanen, Weiler, Moyle, & McLennan, 2015).

Anthropological studies on this type of tourism have explored the cultural legacy of key terms such as ‘authentic’, ‘sustainable’, ‘nature’, and ‘wilderness’, which are often derived from Western understandings of colonial expansion and an industrial/wilderness dichotomy (Cater, 2006; Knight, 2000; West & Carrier, 2004). Since these concepts underpin many of the commodified images of tourist destinations designed for Western travellers, their implications for host communities and the surrounding environment are crucial to an understanding of the burgeoning ecotourism industry (Hall, 2016).

At its core, tourism is often described as the production of experiences (Chambers, 2010). Advocates of ecotourism argue that it offers experiences with the natural world, ostensibly in a way that provides economic benefits for host communities while reducing the negative impact of travelling on the environment (Fletcher, 2015). Ecotourism ventures also claim to prioritize the education of host communities, foreigners, and local tourists, rather than simply offering experiences for consumption by participants (Honey, 2008). Ecotourists themselves may be motivated by a desire for accomplishment (e.g. summiting a mountain), personal growth, or a desire to provide financial support for what they perceive

to be ethical, sustainable tourism (Fletcher, 2015; Hindley & Font, 2018; Igoe et al., 2010). However, ecotourism, just like tourism more broadly, has the potential to negatively impact local communities, infrastructure, and flora and fauna. There is ongoing debate in the academic literature about whether ecotourism can indeed finance conservation, or whether the benefits of community-based programs are outweighed by structural inequalities and the ever-increasing carbon footprint of international travel (Fletcher, 2019; Hall, 2016; Juvan & Dolnicar, 2014).

3.1.2 Criticisms of Ecotourism

The ability of self-identifying ecotourism sites to protect the local environment, educate visitors, and provide ethical and reliable long-term employment for local residents remains up for debate and will vary widely depending on the location (Chambers, 2010). In reality, these destinations are more likely to satisfy only some of the above criteria because the cost of eco-friendly initiatives may not be feasible for businesses. This is a particular problem where a lack of infrastructure for clean drinking water, recycling, or composting places undue pressure on sites that are struggling to keep guests comfortable while disposing of waste in a sustainable manner (Chambers, 2010; Gössling, Hall, & Scott, 2015; Juvan & Dolnicar 2014).

An understanding of the potential benefits of ecotourism is further complicated by the fact that ecotourists themselves are also a varied group. They may be highly informed and motivated participants seeking intense physically demanding experiences, or they may prefer for a more passive approach to experiencing nature in a broad sense (Soulsbury & White, 2015). Their personal biases may influence their interest in particular animals, their

interactions with local communities, or their interpretation of information they receive while traveling (Fraser & Sickler, 2008; Waters, Bell, & Setchell, 2018). Ecotourism frequently involves an undercurrent of exoticism, where cultures that are referred to as ‘indigenous’ are on display as a part of the ‘natural’ world that is so appealing to most ecotourists (West & Carrier, 2004). Visitors may be either foreign or local, though the price of admission to reserves may preclude local residents from being able to visit (Chase, Lee, Schulze, & Anderson, 1998). Variation in visitor priorities and financial capital combined with a lack of information on local racial and cultural disparities may complicate the goals of ecotourism operators who are also balancing economic and social motivations while limiting their impact on the environment. Business owners are also tasked with navigating relationships between neighbouring communities whose access to traditional natural resources can be limited by the creation of protected areas (Chambers, 2010; Honey, 2008; Nthiga, Van der Druim, Visseren-Hamakers, & Lamers, 2015; Silva & Mosimane, 2014).

Ecotourists from the global north often justify ecotourism as a necessary antidote to stressful full-time employment that removes people from the ‘natural’ world. As such, these vacations often take on a spiritual tone and are seen as an opportunity to ‘reconnect’ with nature (Chambers, 2010; West & Carrier, 2004). There is indeed a growing body of literature on the health benefits of exposure to nature, with avid supporters arguing that increasing separation from nature has negative effects on physical and mental health for both children and adults (Cox et al., 2017; Fletcher, 2015; Soulsbury & White, 2015). The call for more exposure to ‘green spaces’ raises many of the same concerns as the tourist industry in general, that is, that time spent near wildlife may have benefits for human well-being, but wildlife may experience adverse effects due to increased road traffic, noise

pollution, infectious disease, or a host of other potential risks (Honey, 2008; Soulsbury & White, 2015; Woodford, Butynski, & Karesh, 2002).

As conversations on the urgency of biodiversity loss become more common, so too does the desire of tourists to see rare and endangered animals or ecosystems (i.e. *last-chance* tourism) and to share these experiences on personal social media pages (Gössling, Scott, & Hall, 2013; Hindley & Font, 2018; Llodra-Riera, Martínez-Ruiz, Jiménez-Zarco, & Izquierdo-Yusta, 2015). Given the importance of evidence-based policies to protect vulnerable wildlife, we sought to assess the motivations and experiences of visitors to the Sepilok Orang-utan Rehabilitation Center (SORC) and the adjacent Bornean Sun Bear Conservation Center (BSBCC), hereafter referred to collectively as ‘Sepilok’. We aimed to better understand why visitors came to Sepilok, what their prior experiences with wild primates were, and how much they knew about infectious disease risk. Improved knowledge of how past experiences with primates might shape visitors’ understanding of animal behaviour and conservation issues will allow sites to address problematic patterns of tourist behaviour that may threaten the animals’ safety.

3.1.4 Study Site

Sepilok is located in eastern Sabah on the island of Borneo. It is easily accessible by car or bus and is a thirty-minute drive from Sandakan International Airport. During the 10-month study period from November 2016 to August 2017, SORC received 159,573 visitors while BSBCC received 59,783 visitors. Income from visitor admissions is put towards the costs of rehabilitation and release, including staff salaries. Both rehabilitation centers lie along the boundary of the Kabili-Sepilok Forest Reserve (5.51841N, 117.57003E); a 55km²

protected area that includes lowland dipterocarp, heath, and mangrove forests (Liu et al., 2018).

Educational signs at the orang-utan center are written in English and they cover a wide variety of topics, including orang-utan life history, the exotic pet trade and its role in creating orphaned orang-utans, the rehabilitation process, and the effects of the palm oil industry on Sabah's forests. Infectious disease is mentioned on only one sign near the ticketing gate. Educational signs at the sun bear center are translated into English, Malay, and Mandarin, and similarly explain the plight of sun bears in the wild which are hunted for the pet trade and traditional Chinese medicine.

Some of the signs at SORC describe the role of orang-utans as seed dispersers in the forest, which reflects the growing trend in ecotourism education where flora and fauna are valued for the services that they provide to humans (i.e. ecosystem services) rather than only their intrinsic worth (Fletcher, 2015). Sepilok itself represents a type of ecosystem service where the forest and the animals within it provide both tourism-based employment and visitor education (Nthiga et al., 2015; Soulsbury & White, 2015). The animals at Sepilok can therefore be seen as a type of commodity that are generating income for their own conservation (Fletcher, 2015; Hall, 2016; Haraway, 2013).

Due to Sepilok's liminal state as a location that appeals to ecotourists, organized group tours, and everyone in between, it attracts a wide range of visitors with varying interests, educational backgrounds, travel experience, and socioeconomic statuses. Sepilok may not offer visitors the ability to sleep in a rustic lodge beneath a mosquito net or learn about local cultures, but its commitment to conservation and ability to offer experiences with rare and endangered wildlife are in line with ecotourism's core principles. Sepilok's

ability to limit visitors' impact on the local environment is largely related to their effort to prioritize animal well-being. The provisions given to both the orang-utans and the sun bears are under strict control of the staff. Visitors are not permitted to eat or drink in either the orang-utan or sun bear center, limiting the amount of garbage that makes its way into the forest. Smoking and vaping are also prohibited. Visitors are restricted to the pathways and boardwalks at each center, which limits their ability to damage naturally occurring flora.

3.2 *Methods*

I conducted 22 semi-structured interviews using open-ended questions in order to learn more about visitors' motivations for visiting Sepilok, their prior experience with primates, and their perceptions of local conservation risks (see Appendix 3.1). Eleven of those interviews were conducted with single individuals, fourteen with pairs of visitors, and one was with a group of three travelling together (N=42). Since all educational material at the orang-utan center was in English, interviews were likewise limited to English speakers in order to see what people remembered from the signage. Most interviewees hailed from Western countries, including the UK, Ireland, Canada, the United States, Spain, and Australia (see Appendix 3.2). Participants were informed that they could stop the interview at any time or skip any questions that they did not want to answer. Interviews were conducted throughout October and November 2017, and took place between 1600 and 1700h so that interviewees had the chance to attend both the morning and afternoon feeding at the orang-utan center, as well as the sun bear center (if they had decided to do so).

I also observed tourists over the course of my 10-month study as I followed the resident hybrid group of long-tailed macaques (*Macaca fascicularis*), pig-tailed (*M.*

nemestrina) macaques, and their hybrid offspring. Combined with the three months that I spent finishing microscopy work and conducting the interviews reported here, I spend an estimated 420 hours in the vicinity of tourists at Sepilok over a period of 13 months. Time spent on the viewing platforms and boardwalks at both rehabilitation centers and inside the canteen afforded me the opportunity to listen to tourists without disclosing that I was a researcher. I did not systematically observe individual visitors, but rather, made notes of their behaviour when approached by orang-utans or macaques (see chapter 4) and wrote down candid comments about the animals, the centers, staff behaviour, and prior experiences with wildlife. Participant observation data was used to develop the questions featured in the semi-structured interviews reported here and to inform the subsequent discussion of actual versus reported tourist behaviour. This study was conducted in compliance with the non-medical research ethics board at the University of Western Ontario (see Appendix 3.3; protocol #109478). This project also had the approval of the Sabah Biodiversity Council and the Sabah Wildlife Department.

3.3 Results

3.3.1 Opinions of Tourists about Orang-utans

The majority of the participants responded that they came to Sepilok specifically to see the orang-utans (20/22, 91% of interviews). One couple said that they were there to see wildlife in general, and one other person was there to see the sun bears after having visited the orang-utans earlier in the week. No one reported being primarily motivated to see flora.

When asked what they thought of the orang-utans, respondents uniformly described the animals favourably. Several people commented on how they enjoyed watching the

orang-utans because “they’re just like us.” Comparisons to humans and, more specifically, human-like movement were common. The beauty and rarity of the orangutans was another theme across interviews, with people claiming they enjoyed seeing the orang-utans because of their beauty, their status as an endangered species, and because they were so different from any other wildlife. One woman described the orang-utans in radiant, familial terms one day after an orang-utan had taken and damaged her phone:

“I just think they’re fabulous. I think it's just like the man of the forest thing and apparently they're our closest relatives aren't they, as far as primates go? ... I think I just wanted to come see them really. Cousins, you know?” (Woman in her 50s, United Kingdom).

Positive, empathetic comparisons between humans and primates were common during participant observation on the viewing platforms, and often focused on mother-infant relationships. During participant observation, visitors commented on “how tired mom looked,” how human-like the babies were, or how the women “remembered those days” of carrying and nursing infants. Although most respondents had nothing but positive things to say about orang-utans, I also occasionally overheard people make self-deprecating remarks or tease their friends or family by making comparisons to the primates:

Woman: I’m telling you, you look just like him [pointing to an orang-utan].

Man: Nah, get out of here [laughing].

Woman: [laughing] You do. Your hair is just the right colour.

3.3.2 Opinions of Tourists about Macaques

Macaques, on the other hand, were often described using anthropocentric language that involved thievery (Knight, 2000), though this was usually by people who had seen them previously at one or more sites where rates of physical contact and macaque aggression towards humans were high. Much like other pest species, these “cheeky” or “naughty” macaques were described as trying to “steal”, “pinch”, or “grab” food and personal belongings at tourist sites in places like Bali or Sri Lanka. Several of these people were wary of macaques after either being threatened themselves or observing others being threatened. A couple travelling together described this pattern when I asked them whether they liked being close to macaques:

Woman (27 years old, United Kingdom): We didn’t like them. Because the ones in Thailand tried to grab anything—grabbed his glasses case and started eating it and then tried to run after us.

Man (28 years old, United Kingdom): Yeah, the one chased after me.

Woman: So then the ones in Kuala Lumpur we just tried to avoid.

On the other hand, visitors who had not seen primates in the wild before did not appear to take much notice of the macaques. They often failed to mention that they had seen macaques at all when I asked what animals they observed at the center and only recalled having encountered macaques after I prompted them. Most of these interviewees did not have anything positive or negative to say about the macaques, nor did anyone report being

on the receiving end of aggression or theft attempts during their time at Sepilok. Perhaps unsurprisingly, the sense of relatedness to orang-utans that came up during several interviews was never mentioned while discussing macaques.

3.3.3 Disease Transmission and Conservation Issues

Although several tourists claimed they had thought about the risk of disease transmission between humans and primates, few offered specific information about how or what diseases might be spread. People generally focused on physical contact as the only risk factor. There was little talk of aerosol transmission and no mention of the risk of shared surfaces or chronic physiological stress. As one woman stated: “I would just be careful not to encourage closeness and avoid them.” (46-year-old woman, New Zealand).

This woman showed a good understanding of the importance of maintaining distance from the animals, and she was glad that they did not see more orang-utans because it meant that the rest were “off in the forest”. Although she did not get close to an orang-utans, in general, avoiding well-habituated primates is easier said than done in a crowded area where they have the benefit of arboreal movement. Interestingly, a couple that witnessed a juvenile orang-utan hanging from a rope and attempting to urinate on tourists did not associate bodily fluids with disease risk. Like most of the other tourists, they were focused on direct contact as something to be avoided.

In nearly one-third of interviews ($n=7$), respondents said that they had never thought about primates and disease until they saw the staff wearing face masks, gloves, and rubber boots, or were asked to use hand sanitizer at the ticket gate:

I don't worry about it, it didn't occur to me until I saw the masks they've got on when they're feeding the orangutans, and then I recalled what I've read about giving animals diseases. And of course, tribal people as well we've done the same. (46-year-old woman, New Zealand).

I never thought about it until I saw the guys with the masks. And I thought *yeah of course*. (67-year-old woman, New Zealand).

This personal protective equipment, then, serves two important functions: it limits the risk of pathogen transmission between the orangutans and their keepers, and it also signals to otherwise oblivious tourists that they should be concerned about infectious disease.

When asked to list threats to primate livelihood in Sabah, respondents identified general deforestation most frequently (14), followed by palm oil (12), poaching or pet trade (6), humans (5), disease (2), and tourism (1). Two people could not think of a threat. One such guest who acknowledged he had never really thought about disease as a risk proceeded to tell me a story about how he ended up with a long-tailed macaque's tail in his mouth after one climbed onto his shoulder at Padangtegal temple in Bali.

The responses to this question may reflect the efficacy of the educational signs around the center, as several people recalled learning from the educational material that orang-utans have a long life history, which negatively affects their conservation . Visitors also recalled information on how the palm oil industry was driving deforestation, resulting in decreasing numbers of orangutans in the wild.

3.4 Discussion

3.4.1 You Can't Always Get What You Want

The paradox of ecotourism is that it proposes that financial incentives can protect fragile ecosystems and even mitigate damage done by the very profit-driven systems that led to habitat degradation in the first place (Fletcher, 2015; Gössling et al., 2013). This can be described as a form of *disaster capitalism* (similar to last-chance tourism) that drives the ecotourism industry because tourists are motivated by the desire to see nature before it disappears due to capitalist expansion (Fletcher, 2019). In an ecotourism context the cause of, and cure for, conservation issues are the same. Several visitors to Sepilok commented that they primarily wanted to see the orang-utans precisely because they were endangered. In doing so, however, they benefit from the very expansion of infrastructure that is a result of the palm oil industry, which caused large-scale habitat degradation in the first place (Parreñas, 2018).

Sepilok further highlights the problems associated with ecotourism initiatives that offer encounters with wild or semi-wild animals because many guests may expect to see a certain number of animals or to see them at a close distance. I often overheard people lament about how many other visitors were at the orang-utan and sun bear centers, and it was common to hear thinly-veiled boasts about preferring to see animals in the wild instead of in a zoo. The gap between expectation and reality lies in the fact that people do not come to Sepilok for a multi-day trek into the forest where they will have the opportunity to view completely wild orang-utans free from large crowds. Viewing these animals in the wild simply does not afford the same visibility or opportunity to observe multiple orang-utans of various ages. As one visitor put it:

I did get to get close to them, but actually I enjoy seeing them more in the wild. Since it was my last day, I thought I'd come to see them.... you know if they're in the forest up in a canopy you don't get a good look. You take a photograph and then you realize oh it's just a leaf. (67-year-old man, United Kingdom).

The priorities of visitors frequently appeared to be contradictory: people want good pictures and the chance to get close to the animals, but they do not want to be exposed to crowds. This contradiction harks back to Chambers' (2010) notion of aesthetic harmony, whereby large numbers of people conflict with the ecotourists' desire for a pristine natural landscape devoid of human influence. Many visitors to Sepilok seem to want 'authentic' experiences with nature where they can get close to orang-utans and sun bears while being isolated from other visitors—all without setting foot on the forest floor. The rehabilitation centers are tasked, then, with trying to put the interest of the animals first by keeping tourists from getting too close while also managing varying expectations regarding what constitutes a satisfying encounter with nature (Fletcher, 2015).

3.4.2 Perceptions of Primates

Although the majority of the participants in this study came from Western countries (95%, $n=35$), Asian and southeast Asian visitors to Sepilok make up more than half of all attendees annually (S. Alsisto, personal communication, August 31st, 2019). Close encounters with primates are likely to cause a wide range of reactions among visitors to Sepilok given the fact that Western interpretations of primate taxa differ widely from those

found throughout Asia, where religious and traditional beliefs have shaped the relationship between people and primates for centuries (Fuentes, 2012). Centuries of European folklore depicting apes and monkeys as unintelligent, wild brutes may well have shaped tourist perceptions of orang-utans that are at once majestic and laughable (Wheatley, 1999). For example, visitors' tendency to describe orang-utans in glowing terms while also jokingly comparing them to friends or family also reflects ethnographic research on other primates who occupy a liminal state; they are neither human nor animal, so they are spoken of in multiple, seemingly contradictory, ways (Waters, Bell, & Setchell, 2018). Another example of this pattern comes from Morocco, where shepherds often joked about the similarities between their peers and the local Barbary macaques (*M. sylvanus*) when interviewed as a group. When spoken to privately, however, they focused more on the metamorphosis of macaques as former humans (Waters, Bell, & Setchell, 2018). Both of these examples demonstrate the ability for primates to be both admired and mocked during the same encounter.

The apparent disdain for macaques at Sepilok raises interesting questions about which animals tourists believe should be present in protected areas, such as the Kabili-Sepilok Forest Reserve. Ultimately, negative interactions between humans and primates often stem from divergent beliefs between two or more groups of people about the value of a given species, the amount of autonomy people have over natural resources, or feelings of exclusion from political and conservation policies (Humble & Hill, 2016). In this tourist environment where the majority of visitors are not from eastern Sabah, opinions on the inherent value of a species seem to guide behaviour compared to feelings of exclusion from decision-making. Tourists who had experience with macaques in the past did not seem to

be entertained by thievery or chasing behaviour. This is in stark contrast to the woman who gleefully recounted the story of her new phone being stolen and damaged by an orang-utan during an encounter where no staff members were present. It is the same bold and resourceful nature of macaques that allows them to thrive in myriad environments and earns them a less-than-favourable reputation at places like Sepilok. The animals are blamed for their behaviour rather than recognizing the social and economic conditions that led to their interactions with people in the first place (Parreñas, 2018).

3.4.3 Understanding of Conservation Issues

Though it is tempting to assume that visitors who are aware of environmental issues will make for more educated and eco-conscious tourists, environmental awareness in a tourists' home country does not guarantee that a person will be aware of, or interested in, the large- and small-scale negative effects of their travels (Becken, 2004). This cognitive dissonance may result in people ignoring facts about the impact of travelling, such as the large carbon footprint associated with long-haul flights, or justifying their decisions based on predominantly responsible environmental behaviour at home (Juvan & Dolnicar, 2014).

The same effect could help explain tourists' behaviour that is potentially harmful to wildlife and yet remains steadfastly difficult to curtail, such as the desire to get close to the animals.

There are several factors associated with global biodiversity loss that are also tied to tourism, such as land clearing and pollution (Hall, 2016). Although guests to Sepilok were quick to identify land clearing due to palm oil as a threat to wildlife, only one visitor stated that tourism had a negative effect on local wildlife due to the need to clear land for accommodation and roads. Predictably, no one mentioned the global impact of the tourism

industry as a factor affecting conservation issues in Sabah. A total of eight (36%) respondents felt that supporting tourism was a good way to help alleviate the issues plaguing orang-utans in the wild, though no one connected tourism to the consumption of palm oil, which is used locally as a cooking oil. Only one couple mentioned ecotourism specifically; they were also the only ones to report that they were in Sepilok to see wildlife in general, not just orang-utans. They said that they could help by:

Support[ing] tourism and places like this—being conscientious about where you're staying so that you're helping the locals. We're staying, you know, where locals work and on the river we're staying with the locals. And you know, to show people that there's more to life than plantations for making a living. (52-year-old woman and 56-year-old man, United Kingdom).

This opinion represents another type of contradiction seen in tourists; that is, they often do not want to see signs of poverty or prosperity (Chambers, 2010). While it is uplifting to hear that visitors are learning about some of the problems associated with the palm oil industry, 36% of interviewees stated that avoiding palm oil was a way they could help. This may be a logical answer, but it is not necessarily in line with recent policy reports on palm oil best practices, which argue for a focus on the importance of monitoring wildlife populations near plantations, minimizing further land conversion, and supporting community access to natural resources in order to reduce the environmental impact of this high-yielding crop (Meijaard & Sheil, 2019). Ideally, visitors to Sepilok and other sites throughout Borneo should leave with a better understanding of the complexity of the palm

oil industry, including the danger of shifting the global demand for oil towards higher latitude crops that will require considerably higher rates of land conversion (HCS, 2015).

When I asked the same couple whether or not they had been to nearby Labuk Bay, a proboscis monkey (*Nasalis larvatus*) sanctuary, they replied that they had, and that they had given advice to another tourist about it:

We were speaking to a woman today and she wasn't sure if she wanted to go [to Labuk Bay] just like we weren't, but we thought no, you've got to show people that there's other ways to make money [than just palm oil]. We think eco-tourism is great, there's nothing wrong with it, the more that they're aware of it the better. (52-year-old woman and 56-year-old man, United Kingdom).

While this couple was echoing one of the main tenets of ecotourism—that it provides employment for local communities—the example of Labuk Bay is not what most experts would call educational or sustainable tourism. The center is owned by an oil palm plantation owner and located within an oil palm estate. I have heard numerous stories of people touching and feeding the primates, which include proboscis monkeys and silver langurs.

Ideally, ecotourism enterprises should build on nearby projects with an eye for long-term viability rather than displaying animals in a kind of glorified zoo (Nthiga, et al., 2015). Simply demonstrating that wildlife can be profitable is not the same as encouraging environmentally-aware ecotourism ventures that prioritize the well-being of local flora and fauna and educate visitors about conservation issues. As of September 2019, admission to

Labuk Bay for non-residents is approximately double the price of either SORC or BSBCC and it does not include rehabilitation and release as a part of its objectives. It certainly does not stand to reason that all tourist locations that purport to help animals are striving to follow the ecotourism model of putting sustainability above profit.

3.4.4 Take Nothing but Pictures, Leave Nothing but Footprints

A minority of respondents ($n=3$) mentioned that they were not upset to have seen few animals because they recognized that that meant the orang-utans were “off in the jungle.” During participant observation, I heard several people complain about how far away the animals were, how few were around, or the fact that observing the juvenile orang-utans at the nursery felt like a zoo.

Research into both conscious and subconscious motivations for travelling has suggested that self-centered values, such as the need to satisfy personal goals or achieve a sense of self-fulfillment, may drive tourist behaviour even when these motivators are not made explicit (Hindley & Font, 2018). No one mentioned photography as a primary motivator for visiting Sepilok, but their *self-centered* behaviour (i.e. lacking consideration for broader community goals) suggests that the desire for good photographs is an important motivator for tourist behaviour (Halman et al., 2008). While I witnessed many people take advice from staff and back away from the orang-utans and macaques, I also watched people ignore these warnings equally often, or heed the advice only *after* they had taken their pictures. I frequently watched people position themselves or their children within an arm’s reach of adult orang-utans in order to take a good picture. Public images shared on Instagram under the tag #Sepilok support these observations, with dozens of images

illustrating the extent people will go to in order to get a good picture with the animals. This user-generated content may serve as a motivation for undesirable behaviour for people at Sepilok, but it also sets expectations for future visitors (Llodra-Riera et al., 2015). One woman told the story of how she was taking pictures of a male orang-utan before he took her phone up a tree and chewed on it for the better part of two hours while “trying to take selfies”:

“He [the orang-utan] actually went up to this chap and stuck his tongue in his belly button and then climbed up him and tried to get a bit fresh with him and then the man pushed him away and then he came and just snatched me [sic] phone, but [it] had a [ring] on the back and I had me [sic] fingers through it and I couldn't let go, so for about 30 seconds I actually grappled with this orangutan to try to get me [sic] phone back, but the [ring] came off the phone and went flying over the railing. So I knew I had to let go because he actually bared his teeth to this chap. So I don't know if that is indicative of something ... so I thought *let it go*. So he just took it.”

(Woman in her 50s, United Kingdom).

She told me how her phone was covered in saliva by the time the orang-utan gave it up. When I asked her if she had ever thought about primates getting diseases from humans, she told me that she was aware it was a risk and that she probably should have sanitized her phone after getting it back. She also mentioned that she had a cold the previous week and could feel a cold sore starting. She said that she probably would not have visited if she had gotten worse. While this sounds like responsible behaviour, it is entirely possible that she

was still infectious despite no outward signs of illness. This example is also particularly concerning given that mobile phones have been shown to be a significant public health risk due to their ability to transport pathogens such as *Shigella* spp. (Jeevanaraj, Aluwaisi, & Ismail, 2018).

All ecotourism sites should, in theory, attempt to balance the priorities of the host community and visitors while reducing the impact on surrounding flora and fauna (Honey, 2008). Sepilok (and other rehabilitation sites like it) are particularly complex because the animals' behaviour is unpredictable. The mantra "take nothing but pictures, leave nothing but footprints" is insufficient guidance in a setting where semi-habituated animals are free-ranging and considerably stronger and faster than the visitors around them. The same can be said of macaques, who are well-habituated and more likely to approach visitors to Sepilok compared to groups that might be encountered on a remote jungle trek. This highlights the importance of staff guidance because visitors may underestimate the danger of being too close to these wild primates, especially because visitors said they thought the orang-utans looked "relaxed"; a precarious and subjective state that may change suddenly when an animal becomes agitated.

3.4.5 Visitor Understanding of Disease

Visitors' fixation on direct contact as the main mode of transmission reveals a fairly rudimentary understanding of infectious disease that should be expected from non-specialists. Although direct contact is certainly relevant in a tourism context, aerosol and bodily fluids are responsible for many of the most severe examples of primate mortality, such as tuberculosis (Gilardi, Gillespie, & Leendertz, 2015; Keet, Kriek, Bengis, Grobler,

& Michel, 2000) and rhinoviruses (Muller, Wrangham, & Pilbeam, 2017). There are also multiple contemporary examples of insect vectors causing serious emerging infectious disease risks in humans, including malaria and zika virus (Singh et al., 2004; Stark et al., 2019; Weber, Alroy, & Scheiner, 2017).

Two people that I interviewed underestimated their ability to spread disease because they associated their own lack of symptoms with overall health:

I've learned about humans they bring viruses to pets ... in my own experience I'm healthy so I guess I didn't bring any harm to them. As long as I didn't sneeze, I wouldn't give them any harm. (24-year-old woman, Malaysia).

However, an absence of symptoms does not necessarily imply an absence of risk because visitors may experience asymptomatic shedding, i.e. they may be infectious without feeling ill (Patrono, 2018). These misunderstandings about the complexity of infectious disease risk may be a contributing factor to many tourists' reluctance to keep their distance from wild primates, especially when the opportunity to get a photograph next to these animals is so tempting.

Social media allows researchers to explore tourist behaviour beyond what they witness themselves. A search for user-generated content under the tags #Sepilok, #MonkeyTemple, or #BatuCaves on Instagram reveals dozens of people taking pictures of themselves with wild orang-utans and macaques. These pictures frequently involve close proximity or even direct contact, and they reflect an on-going threat in conservation education and tourism: how do we encourage people to change their behaviour?

Research on gorilla tourism in Uganda found that negatively-framed signs that highlighted the severe risk of infectious disease to gorillas were more effective at changing tourist behaviour than neutral or positively-framed signs (Gessa & Rothman, 2016). Pointing out the dangers that tourism poses to wildlife more explicitly may be an effective way to change undesirable behaviour rather than simply hoping people will move away when asked (Juvan & Dolnicar, 2014). Comments from visitors during interviews suggest that visual cues, such as rubber gloves, hand sanitizer, and face masks were effective at conveying basic information about infectious disease being a risk factor at Sepilok.

A little more than half of respondents (57%) reported that they would be looking for more primates during their travels either within Sabah or in neighbouring southeast Asian countries, such as Indonesia or Thailand. Given that both of these places are known for facilitating close contact between tourists and macaques (Fuentes et al., 2006), one would hope that a better understanding of the risks of disease transmission to primates might encourage more responsible behaviour in the future.

3.5 Conclusions

Visitors do appear to learn about orang-utan life history, the negative effects of the palm oil industry, and basic facts about infectious disease transmission at Sepilok. However, the extent to which they are leaving with an improved understanding of how they can positively impact change is unclear. This begs the question of how much tourists should be learning if a site is to be characterized as ‘ecotourism.’

As a site that attracts ecotourists, Sepilok is something of a mixed success. The low rate of human-directed aggression from macaques is a step in the right direction compared to many other popular tourist sites throughout Asia. However, there is certainly room for

improvement when it comes to reducing the frequency with which visitors are able to get close to the orang-utans and the degree of visitor understanding of infectious disease risk upon leaving the centers. Places like Sepilok will need to continue to mitigate the desires of visitors who may value the environment broadly, but who may not appreciate what behaviour is appropriate for a given location or species (Knight, 2000).

It is easy to shame tourists for wanting to get too close to wild primates, but it is also unreasonable to expect non-specialists to have an understanding of the epidemiology of anthrozoonotic diseases. Tourists are unlikely to see the negative effects of infectious disease or long-term changes to primate ecology and life history as a result of tourism, so it is understandable that they may not consider themselves to be a part of the problem (Galbraith et al., 2014; Hall, 2016). With such unrelenting pressure for sites to satisfy tourists' expectations for meaningful (or perhaps *Instagrammable*) experiences (Llodra-Riera et al., 2015), protecting the well-being of the animals and the surrounding environment becomes increasingly difficult. Photographs are an important part of the visitors' experience, so any new education techniques should specifically address undesirable photography behaviour.

At the micro level, most visitors to Sepilok simply want an encounter with charismatic and endangered species and to learn a little about local conservation issues. However, these tourists (eco- or otherwise) are a part of a complex socio-political system that integrates conservation biology, ecology, resource extraction, socio-economic status, and long-standing colonialist and capitalist histories (Hall, 2016; West & Carrier, 2004). The question of who has access to these spaces, what resources these spaces use, and their ultimate impact on the immediate environment and broader conservation initiatives is

obscured by visitors' preoccupation with simple solutions to multifaceted problems. We can address these issues by ensuring that visitors are educated on all of the risks facing endangered species, including the risks associated with tourism itself. Rehabilitation sites such as Sepilok must continue to weigh the potential to inconvenience tourists by limiting their proximity to wildlife against the benefits of the well-being of at-risk species.

3.6 Appendices

Interview Number	Age	Sex	Country of Origin
1	49	F	United States
	26	M	
2	30	F	United Kingdom
3	60	M	The Netherlands
4	70	F	United Kingdom
	72	M	
5	44	F	United Kingdom
	44	F	
6	27	M	Spain
	28	F	
7	67	M	United Kingdom
8	27	F	United Kingdom
	26	M	
9	30	F	United Kingdom
	29	M	Ireland
	32	F	Ireland
10	23	F	Canada
	23	F	
11	24	F	Malaysia
12	46	F	New Zealand
13	52	F	United Kingdom
	56	M	
14	50s (did not specify)	F	United Kingdom
15	67	F	New Zealand
16	22	F	Australia
	22	M	
17	28	F	United Kingdom
	30	M	
18	27	M	Germany
	26	F	
19	31	F	United States
	34	M	
20	34	F	Malaysia
21	40	F	United Kingdom
	42	M	
22	35	F	United Kingdom
	33	F	

APPENDIX 3.1. Summary of all interview participants.

APPENDIX 3.2. Semi-structured interview questions.

1. Why did you come to Sepilok?
 - a. What animal do you hope to see the most?
2. Have you seen wild primates before?
 - i. Where?
 - ii. What did you think of them?
 - b. Have you ever had primates touch you?
 - i. Did they hurt you?
 - ii. Did you like being close to primates? Why?
3. Can you name some of the top risks to primates in Sabah?
4. What animals have you seen so far today?
 - a. Have you been to the sun bear center?
 - b. Will you go?
 - c. Did you see macaques anywhere?
 - d. What has been your favourite animal that you have seen? Why?
5. Can you remember something you learned from the signs around the centers?
6. Did you get close to the primates?
 - a. Was there a staff member present?
 - b. Did they give you any instructions?
 - c. How did you respond?
 - d. Did the primate touch you?
 - e. How did you feel?
 - f. How did the primate seem?
 - g. Did any of the primates take something from you?
 - i. If yes, what?
7. Did you use hand sanitizer when you had your ticket stamped before the feeding?
 - a. Do you worry about catching diseases from primates?
8. Have you been to Labuk Bay?
 - a. Did you feed the primates?
 - b. Touch them?
 - c. Will you look for more primates while you are travelling?
 - d. Is there anything else you want to add about your experience today?
 - e. Do you have any questions for me?

APPENDIX 3.3. Letter of Approval from Western Non-Medical Research Ethics Board.



Research Ethics

**Western University Non-Medical Research Ethics Board
NMREB Delegated Initial Approval Notice**

Principal Investigator: Dr. Ian Colquhoun
Department & Institution: Social Science\Anthropology, Western University

NMREB File Number: 109478
Study Title: The Effects of Ecotourism on the Ecology and Parasite Prevalence of hybrid macaques in Sabah, Malaysia

NMREB Initial Approval Date: September 27, 2017
NMREB Expiry Date: September 27, 2018

Documents Approved and/or Received for Information:

Document Name	Comments	Version Date
Revised Western University Protocol	Received September 25, 2017	
Revised Letter of Information & Consent		2017/09/25
Other	Questions for participants	2017/07/21
Wallet Card	Business card	2017/07/21

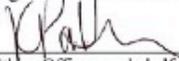
The Western University Non-Medical Research Ethics Board (NMREB) has reviewed and approved the above named study, as of the NMREB Initial Approval Date noted above.

NMREB approval for this study remains valid until the NMREB Expiry Date noted above, conditional to timely submission and acceptance of NMREB Continuing Ethics Review.

The Western University NMREB operates in compliance with the Tri-Council Policy Statement Ethical Conduct for Research Involving Humans (TCPS2), the Ontario Personal Health Information Protection Act (PHIPA, 2004), and the applicable laws and regulations of Ontario.

Members of the NMREB who are named as Investigators in research studies do not participate in discussions related to, nor vote on such studies when they are presented to the REB.

The NMREB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000941.


Ethics Officer, on behalf of Dr. Randal Graham, NMREB Chair or delegated board member

EO: Erika Basjle Grace Kelly Katelyn Harris Nicola Morphet Karen Gopaul Patricia Sargeant Kelly Patterson

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Chapter Four

4 Tourist Behaviour Predicts Macaque Reactions at the Sepilok Orang-utan Rehabilitation Center

4.1 Introduction

The travel and tourism industries are among the largest sources of employment globally and they generated an estimated \$7.6 trillion in 2016 (WTTC, 2018). The extent to which tourism will affect local communities and ecosystems depends largely on the type of experience being offered; ecotourism, or nature-based tourism, has been heralded as a form of sustainable tourism development and represents an ever-expanding portion of tourism revenue in many tropical countries (Brandt & Buckley, 2018). This is particularly relevant for the well-being of non-human primate species (hereafter ‘primates’), who are the frequent focus of such tourism initiatives. As nature-based tourism has become more established throughout primate habitat countries, researchers have justifiably questioned the potential harmful effects of the regular exposure of primates to humans (Jones-Engel, Engel, & Schillaci, 2005; Muehlenbein et al., 2010; Muehlenbein & Wallis, 2014; Russon & Wallis, 2014; Wallis & Lee, 1999). Research on primate-based tourism typically focuses on changes in patterns of primate foraging (McKinney, 2011), social behaviour (Treves & Brandon, 2005), primate aggression towards humans (Fuentes & Gamerl, 2005), risks of habituation (Williamson & Feistner, 2003), as well as qualitative and quantitative indicators of health (Klegarth et al., 2017; Maréchal, Semple, Majolo, & MacLarnon, 2017; Schillaci et al., 2010). Both ethnographic and quantitative methods lend themselves to the study of tourist behaviour, which is influenced by myriad factors. These complimentary approaches

have been used to assess visitors' perceptions of nature (Cox & Gaston, 2018), their behaviour (Maréchal, MacLarnon, Majolo, & Semple, 2016; McCarthy et al., 2009), their awareness (or lack thereof) of risk and their overall health and vaccination status (Muehlenbein et al., 2008). Each of these lines of inquiry is important for understanding the underlying motivations, behavioural patterns, and infectious disease risk of tourists seeking experiences with primates.

Researchers who have investigated wildlife tourism, particularly primate-based tourism, have often focused on the risk of disease transmission, which is higher compared to other taxa because of the close evolutionary relationship between humans and other primates (Wolfe et al., 1998). Many pathogens have evolved within our Order, which means that they are capable of moving between species under the right conditions (Muehlenbein et al., 2014; Taylor, Latham, & Woolhouse, 2001). Tourism can facilitate this disease transmission by encouraging frequent contact between primates and both foreign and local tourists. The amount of contact between species will vary depending on the degree to which staff attempt to limit undesirable or unsafe behaviour from tourists. Staff intervention is high, tourist behaviour is restricted by rules that have been established to protect the health and safety of both humans and primates. Generally speaking, provisioning by tourists, close contact between primates and tourists is avoided, and no effort is made to restrict the range of the primates (see Goldsmith, 2014; Hanes, Kalema-Zikusoka, Svensson, & Hill, 2018).

At sites with low staff intervention, primates often interact with tourists in environments where provisioning is encouraged, direct contact inevitable, and primate aggression towards humans frequent (see Berman, Matheson, Li, Ogawa, & Ionica, 2014;

Wheatley, 1999). The long-tailed macaques that reside near Hindu temples in Bali are an example of low intervention tourism. The macaques are provisioned throughout this temple complex several times per day by the local staff (Brotcorne, Fuentes, Nengah Wandia, Beudels-Jamar, & Huynen, 2015; Fuentes, 2006). Tourists are also not only permitted but encouraged to feed the animals. In the event that a macaque steals any personal belongings from a tourist, staff will use small bags of peanuts to coax the monkey to return the item (Peterson & Fuentes, 2018). Primate aggression towards humans by the macaques is frequent, especially when food is present, and minor bites and scratches that break tourists' skin are not uncommon (Fuentes & Gamerl, 2005). See McKinney (2015) for a broader anthropogenic classification system.

Research on macaques and tourism has traditionally taken place at sites with low staff intervention (see Wheatley 1999). This is likely a result of the ubiquity of macaque species throughout Asia, their reputation as pests, and the low conservation statuses of the species most frequently associated with tourist sites: the long-tailed (*Macaca fascicularis*), pig-tailed (*M. nemestrina*), Japanese (*M. fuscata*) and Tibetan macaques (*M. thibetana*) (Eudey, 2008; Malaivijitnond & Hamard, 2008).

The ability for staff to reduce contact between humans and primates has important implications for health and safety given that the risk of open wounds inflicted by primates may increase the risk of disease transmission with humans. Aggression between tourists and monkeys may also increase the likelihood of other injuries; humans may be injured whilst fleeing aggressive monkeys or by the monkeys themselves (Fuentes, 2010; Wheatley, 1999; Zhao & Deng, 1992), and the monkeys might be injured by tourists in retaliation or by staff who may use projectiles (e.g. rocks) to deter unwanted behaviour or

to corral the primates closer to the tourists (Berman et al., 2014; Berman, Li, Ogawa, Ionica & Yin, 2007; Jones-Engel et al., 2005; Riley et al., 2016; Schillaci et al., 2010).

This study explores the nature of interactions between humans and a group of wild macaques at the Sepilok Orang-utan Rehabilitation Center (hereafter ‘Sepilok’) in Sabah, Malaysia where some tourist management strategies are in place, albeit ones that were designed with the health and safety of other animals in mind. In doing so, it is the first to offer insight into the behaviour of macaques at a site where there are strict, effective rules in place to prevent tourists from hand-feeding wild animals. Sepilok is an appropriate location for research on wildlife tourism because it is one of the most popular tourist destinations in Sabah, and previous research at Sepilok found that 15% of visitors were experiencing some symptom of infection, and many were unaware of their vaccination status for common diseases such as Hepatitis A and measles (Muehlenbein et al., 2008; Muehlenbein et al., 2010). The ultimate aim of this research is to make concrete suggestions for tourist management strategies in order to reduce the potentially negative effects of tourism on wild primates.

Given that Sepilok has strict rules to prevent hand-feeding by tourists, we hypothesized that: i) macaque aggression would be less intense and less frequent compared to sites with low staff intervention; ii) there would be an association between specific human behaviours and macaque aggression; iii) human-directed aggression would be more common in sub-adult and adult males; and iv) the presence of human food and food cues would be rare and not associated with increased aggression.

4.2 Methods

4.2.1 Study Site

The Sepilok Orang-utan Conservation Center (SORC) and Bornean Sun Bear Conservation Center seek to rehabilitate and release orphaned orang-utans (*Pongo pygmaeus*) and sun bears (*Helarctos malayanus*), respectively, while educating visitors about local conservation issues. Located in eastern Sabah, both centers are located within the 55 km² Kabili-Sepilok Forest Reserve, which features primarily lowland dipterocarp forests that are partially logged, as well as heath and mangrove forests along the coast. Elevation fluctuates between 0 and 170 m above sea level and the mean annual temperature is approximately 27 °C (Liu et al., 2018). Rainfall averages around 3136 mm (± 921 SD) annually (Margrove et al., 2015). The reserve borders the Sulu Sea to the east and is surrounded by secondary forest, palm-oil plantations, and cash crops (Maycock, Thewlis, Ghazoul, Nilus, & Burslem, 2005).

There are several contexts in which visitors to SORC may encounter orang-utans. Most notably, the twice-daily feedings for free-ranging orang-utans draw the greatest number of visitors. At 1000h and 1500h guests wait on the designated viewing platform and may observe one or more orang-utans visiting the adjacent feeding platform to feed on seasonal fruit and vegetables. The study group and one other group of pig-tailed macaques also feed occasionally on the available food. Visitors may also encounter the free ranging orang-utans around the center on the viewing platforms, boardwalks, and occasionally near the reception area and cafeteria.

The Bornean Sun Bear Conservation Center is immediately adjacent to the SORC. Both centers share a parking lot and canteen, but they operate independently of each other.

Visitors may view the sun bears in their enclosures at any time between 0900 and 1600h, with peak visitation periods following the 1000 and 1500h orang-utan feedings (W. Siew Te, personal communication, September 25, 2016). The macaques also visit this part of the forest reserve frequently to feed on both naturally occurring vegetation and the food provided to the bears by BSBCC staff. In doing so, they routinely come into close contact with tourists in the same manner as occurs at the SORC feeding platforms.

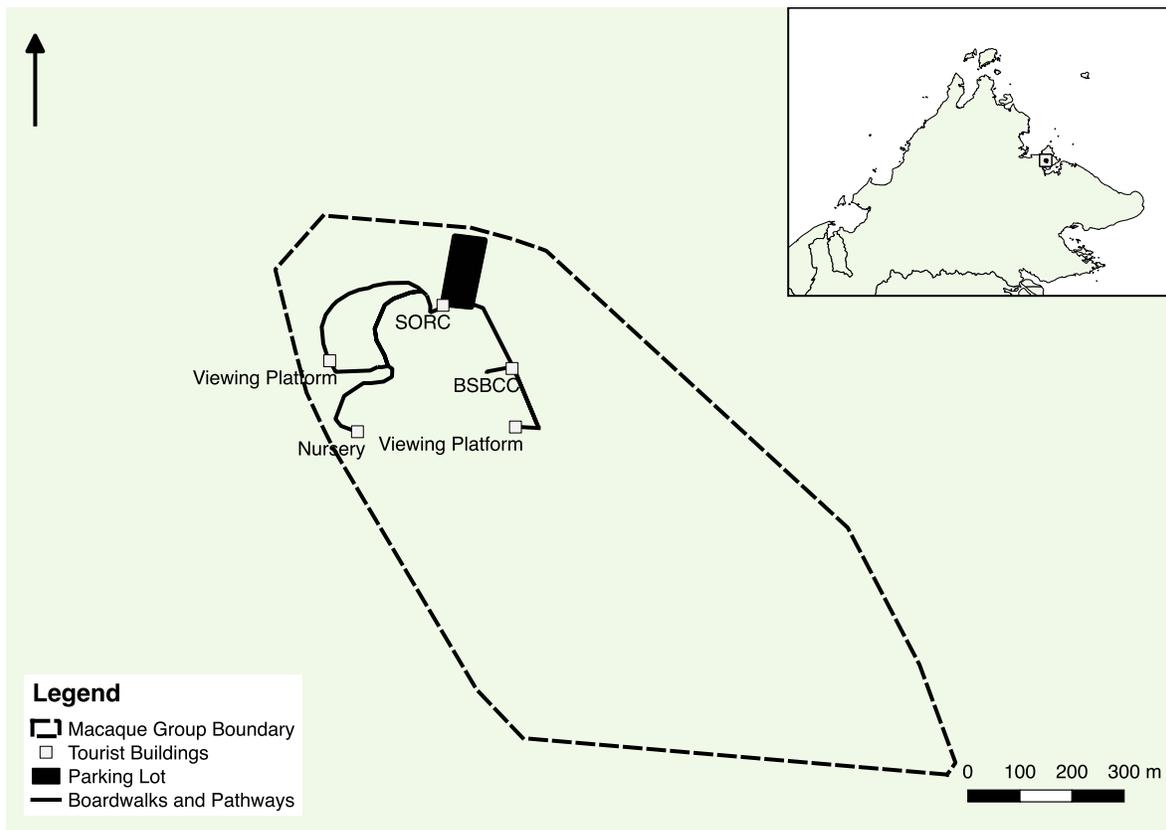


FIGURE 4.1. A map of the SORC and BSBCC, including the areas visited by tourists and an approximate measurement of the macaques' home range (see chapter 5, this volume).

There are strict rules in place at both SORC and BSBCC that limit the ability of tourists to interfere with the animals. Visitors to SORC must leave their belongings near the reception counter and staff patrol the visitor area so that they can monitor any orang-utan that

approaches the viewing platform or boardwalks. The sun bears are housed in large enclosures reminiscent of a traditional zoo. Visitors may keep their belongings with them but cannot reach the bears and they are forbidden from having open food containers or calling out to the animals. There is enough staff supervision at both facilities that these rules are generally enforced without issue.

Interactions between tourists and macaques are slightly different compared to the interactions that tourists have with orang-utans and sun bears. Since the macaques are wild, there are no dedicated staff members to guide visitor behaviour or to intervene in the event of close contact or aggression. Both SORC and BSBCC staff will typically advise tourists to back away from the macaques, but staff are not always present to defuse such encounters or able to change tourists' behaviour.

4.2.2 Study Species

While the orang-utan population at Sepilok is largely the result of the rehabilitation efforts by SORC, there are six naturally occurring primate species present within the reserve: red langur (*Presbytis rubicunda*), Philippine slow loris (*Nycticebus menagensis*), Horsfield's tarsier (*Tarsius bancanus*), northern gray gibbon (*Hylobates funereus*), long-tailed macaque (*M. fascicularis*), and the pig-tailed macaque (*M. nemestrina*). Of these six species, only the macaques take advantage of the provisioned food at the orang-utan and sun bear centers. Proboscis monkeys (*Nasalis larvatus*) are also present on the border of the reserve near the mangrove forests, approximately 7 km away from the rehabilitation centers.

The study group consisted of long-tailed macaques, pig-tailed macaques (*M. nemestrina*) and their hybrid offspring who traveled, foraged, and socialized together daily.

We assessed hybridity based on physical characteristics such as body size, facial morphology, and pelage patterns as well as staff testimony (Figure 4.2). This study group was chosen because it was the only group of macaques that visited the center regularly. There were no groups of long-tailed macaques in the area, and only one other group of pig-tailed macaques that was seen sporadically.



FIGURE 4.2. A suspected first-generation hybrid (left) and a true long-tailed macaque (right). Picture by L. Gilhooly.

4.2.3 Data Collection

We collected data on one hybrid group of macaques for 10 consecutive months from November 2016 – August 2017 within the Kabili-Sepilok Forest Reserve (5.51841N, 117.57003E). The group contained 21 individuals at the beginning of the study period and 23 by the end due to one death, one emigration, and four births. The observational methods

used in this study were adapted from research on human-primate interactions at several tourist sites (e.g. Fuentes & Gamerl, 2005; McKinney, 2014; Ruesto, Sheeran, Matheson, Li, & Wagner, 2010;). We used *ad libitum* sampling techniques during full-day follows to record data on the nature and outcome of tourist-macaque interactions.

We operationalized the interaction between a macaque and a tourist as beginning when at least one tourist and one macaque came within 10 m of each other. For each interaction we recorded the monkey's identification, up to seven data points on relevant human or macaque behaviour, and the outcome. We recorded whether the macaque or human approached the other, the minimum distance that was reached between the macaque and the human, as well as the presence or absence of photography or eye contact. We also noted any human gestures, vocalizations, or food cues. Outcomes were not mutually exclusive, and we recorded the type of macaque aggression, macaque submissive behaviour, human submissive behaviour, or the absence of a reaction. Macaques were not observed making vocalizations towards visitors. Table 4.1 outlines all of the behavioural variables that were recorded, with the exception of minimum distance (Fuentes & Gamerl, 2006; McKinney, 2014; Ruesto et al., 2010).

TABLE 4.1. Ethogram of variations for both macaque and human behaviour.

Behaviour	Type	Definition
Who Approached	Macaque	Macaque approaches a human while they are stationary or moving away.
	Human	Human approaches a macaque while they are stationary or moving away.
Gesture	Point	Human extends their hand towards the monkey.
	Wave	Human waves to try to get the monkey's attention.
	Bend Down	Human bends down to talk to monkey or take picture.
Vocalization	Mouth noise	Human clicks tongue or lips to try to get the monkey's attention.
	Hooting	Human makes a hooting noise or otherwise imitates the monkey's call.
	Talking	Human talks to monkey in normal voice.
	Whistle	Human whistles to monkey.
Take Picture	-	Human takes picture with either smartphone or camera.
Food	Food	Macaque handles human food.
	Food Cue	Human food waste, e.g. empty wrapper.
	Drink Bottle	Macaque handles plastic bottle.
	Wild food	Human offers plant material to monkey, e.g. palm kernel.
Eye Contact	-	Human and macaque meet each other's gaze.
Macaque Aggression	Eyebrow Flash	Macaque raises eyebrows while looking at human.
	Open Mouth Threat	Macaque opens their mouth while looking at human.
	Lunge	Macaque moves either upper body or entire body towards human
	Chase	Macaque pursues fleeing human
	Grab	Macaque takes hold of human or their belongings, e.g. clothes, backpack
Macaque Submissive Behaviour	Fear Grin	Macaque pulls back the corner of their mouth, exposing teeth
	Displacement	Macaque walks out of the way for human
	Flee	Macaque runs or jumps out of the way for human
Human Submissive Behaviour	Scream	Human makes sudden high-pitched vocalization
	Displacement	Human walks out of the way for macaque
	Flee	Human runs out of the way for macaque
No Reaction	-	Neither the human nor the macaque reacts

4.2.4 Statistical Analysis

We used odds ratios to assess patterns between macaque aggression and each of the behavioural variables (approach, distance, gesture, vocalization, take picture, food, eye contact). We collected data on a total of 352 tourist-macaque interactions, although we occasionally missed some human behaviours (e.g. eye contact) because of visual obstructions. Therefore, some tests were run with fewer valid cases. We used Z-scores used to compare rates of aggression between the macaques that exhibited at least one threat towards tourists.

We also used a binomial logistic model, a generalized linear model (GLM), and a generalized linear mixed model (GLMM) to explore the cumulative impact of human behavioural variables on the occurrence of macaque aggression. The binomial model was conducted with and without stepwise regression. We defined human and macaque behaviours as binary fixed effects and aggression was scored as '0' (absent) or '1' (present). The GLMM was defined with the same fixed effects and with macaque ID as a random effect with a random intercept to control for the possibility that some individuals were more aggressive due to demographic or behavioural factors. We used Akaike's Information Criteria (AIC) to compare model fit between the GLM and GLMM. We conducted all statistical tests using SPSS (version 25.0.0.0).

4.3 Results

4.3.1 Age, Sex, and Aggression Type

A total of 352 tourist-macaque interactions were distributed between 19 different monkeys over approximately 250 observation hours where the macaques were within 25m of

tourists. The macaques engaged in visitor-directed aggression at a rate of 0.14 bouts per hour ($n=36$). The five types of aggression exhibited by the macaques are identified in Figure 3. The remaining interactions ($n=316$) did not involve aggressive responses from the macaques. One or more macaques displaced humans during 25.9% of encounters (0.3 times per hour). Tourists did not attempt to frighten, displace, or hurt a macaque either before or after aggressive encounters.

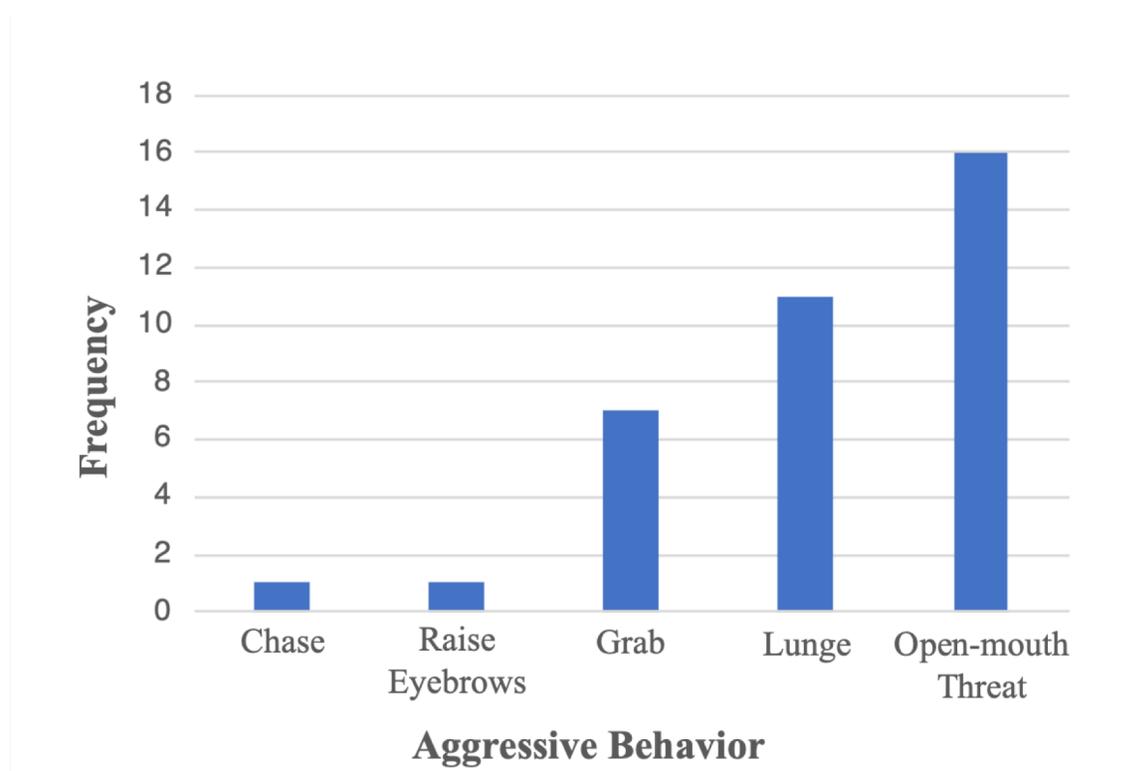


FIGURE 4.3. Histogram displaying the frequency of macaque aggression ($n=36$) during interactions with tourists ($N=352$).

None of the monkeys bit or scratched a tourist, which means that no open wounds occurred as the result of primate aggression towards humans. Macaques grabbed at shirts, backpacks, and hair at a rate of 0.03 incidents per hour, but no skin-to-skin contact occurred during aggressive encounters. All of the direct skin-to-skin contact was the result of one monkey; on 25 occasions, a juvenile female pig-tailed macaque touched tourists' arms or

legs gently as they walked by. These interactions were always peaceful and never resulted in threatening or fleeing behaviour.

Primate aggression towards humans was not distributed evenly between macaques, as outlined in Table 4.2. A single adult male long-tailed macaque engaged in 0.06 aggressive bouts per hour, while an adult pig-tailed macaque was observed being aggressive towards tourists 0.04 times per hour. Together, these two individuals accounted for 66% ($n=24$) of all aggressive incidents recorded ($Z=2.42$ and 1.44 , respectively). Those two macaques were also responsible for the majority of the aggressive grabs that we witnessed (0.02 grabs per hour; $n=5$). In total, adult male macaques participated in 0.10 aggressive bouts per hour (72.2%; $n=26$). A slight majority, 53% ($n=10$), of the monkeys that interacted with tourists were observed to be aggressive at least once (Table 4.5).

TABLE 4.2. Summary of individual participation in aggressive encounters with tourists.

Name	Species	Age Category	Sex	Bouts of Aggression	Aggressive Grabs
Bruno	Long-tailed	Adult	Male	15	4
Bunga	Hybrid	Adult	Female	3	1
Campur	Hybrid	Adult	Female	1	0
Charlie	Pig-tailed	Adult	Male	1	0
Hitam	Pig-tailed	Adult	Female	1	1
Jagindas	Pig-tailed	Adult	Male	9	1
Juvi	Pig-tailed	Immature	Male	1	0
Manis	Long-tailed	Adult	Female	1	0
Pirate	Long-tailed	Adult	Male	1	0
Tabu	Hybrid	Immature	Male	3	0
Total:				36	7

4.3.2 Food

Food was not significantly associated with macaque aggression towards humans, and tourists never tried to offer their own food or garbage to the monkeys. The two attempts by tourists to feed a macaque involved palm kernels that had been dropped by another monkey. The macaque either gingerly accepted the food before discarding it ($n=1$) or ignored the offer ($n=1$). We did not observe aggression towards humans during these feeding attempts, nor did we see any staff present.

On one occasion an adult man was seen holding out his water bottle to a juvenile male macaque, but the man then fled when the macaque lunged at him from 2 m away. On one other occasion, an adult female macaque tried to take a water bottle that had been left on a bench by a preoccupied tourist. These instances occurred at or near BSBCC where visitors are allowed to have their belongings with them.

4.3.3 Human Behaviour and Macaque Aggression

Of the seven data points considered, only two were significantly associated with an aggressive outcome from a macaque. ‘Take picture’ resulted in slightly reduced odds of experiencing macaque aggression (Odds ratio: OR=0.26, $P<0.01$, $N=351$, 95% CI=0.09-0.76), whilst the odds of experiencing aggression following eye contact were significantly higher compared to the absence of eye contact (Odds ratio: OR=15.19, $P<0.001$, $N=315$, 95% CI=6.01-38.40). No tourist tried to pet the macaques or lure them onto their shoulder in order to get a picture.

The binomial logistic model explained 35.6% (Nagerkerke R^2) of the variance in macaque aggression. This model supported the odds ratio tests where only ‘eye contact’

and ‘taking a picture’ were associated with macaque aggression. The model yielded a lower R^2 value (0.358) and a greater reduction in the -2 log likelihood value (112.4) compared to the stepwise regression model ($R^2=0.308$, -2 log likelihood=119.4). The GLM yielded a lower AIC value (62.6) compared to the GLMM with macaque ID as a random variable (1706.1), suggesting that macaque ID did not improve the model. A summary of the model output is provided in Table 4.3.

TABLE 4.3. Results of binomial logistic regression using fixed effects and aggression as the outcome.

Variable	B	Standard Error	Wald	df	p	Odd's Ratio	95% Confidence Interval	
							Lower	Upper
Who Approached	-0.65	0.58	1.26	1	0.26	0.52	0.17	1.63
Distance	0.27	0.17	2.53	1	0.11	1.30	0.94	1.81
Gesture	1.21	0.83	2.08	1	0.15	3.35	0.65	17.35
Vocalization	-1.48	0.93	2.47	1	0.12	0.23	0.04	1.44
Take Picture	-1.81	0.83	4.69	1	<0.05*	0.17	0.03	0.84
Food	-1.34	1.49	0.80	1	0.37	0.27	0.01	4.88
Eye Contact	2.83	0.56	25.59	1	<0.01*	16.97	5.66	50.82
Constant	-3.80	0.71	28.96	1	0.00	0.02	-	-

* Statistically significant value, $p < 0.05$.

4.4 Discussion

The severity and frequency of primate aggression towards humans observed at Sepilok was drastically reduced compared to similar studies on long-tailed macaques at low staff intervention locations throughout Asia. A study by Fuentes and Gamerl (2005) at Padangtegal, Bali, reported that 78% of the observed primate aggression towards humans was classified as ‘intense’, which included all physical contact, such as bites. Simple

threats, on the other hand, accounted for only 12% of the observed primate aggression towards humans at Padangtegal. This is in stark contrast to Sepilok where 47% of the macaque aggression was considered a simple threat, including open-mouth threats and raised eyebrows. Only 19% of the aggression involved direct contact and no biting or scratching occurred. Although the GLMM did not suggest that macaque ID was a significant factor in predicting rates of aggression in this study, the distribution of aggressive behaviour was skewed towards adult males (Table 4.2). The paradox of low rates of human-directed aggression at Sepilok is that a larger sample size is needed to conclusively argue that species and sex differences are present.

The significant results for ‘eye contact’ and ‘taking a picture’ are consistent with previous findings where specific human behaviours predicted macaque aggression (Ruesto et al., 2010). Understanding which human behaviours may elicit aggression from specific macaque age-sex classes in particular contexts is a crucial component to reducing tourist-directed aggression. Here we explore findings on human behaviour and macaque aggression and the potential implications for human and macaque health.

Taking pictures might be associated with lower odds of experiencing aggression at Sepilok because the tourists are likely looking at their phone or through their camera, rather than making direct eye contact, which was associated with significantly increased odds of experiencing aggression (Table 4.3). Others have observed that macaques threaten more when cameras are present; potentially because they see their reflection in the lens (D. Bertrand, personal communication, April 15, 2018). There is some evidence to support this hypothesis given that macaques have consistently failed the mirror self-recognition test and typically react to their reflection socially, rather than recognizing themselves (Anderson &

Gallup, 2015; Gallup, Wallnau, & Suarez, 1980; Mitchell & Anderson, 1993). Social reactions to cameras did not appear to be a trend in this study.

Eye contact or staring between conspecifics has been associated with aggression in a number of macaque species, including long-tailed macaques (Cannon, Heisterman, Hankison, Hockings, & McLennan, 2017; Chance, Emory, & Payne, 1977), pig-tailed macaques (Oettinger et al., 2007), and rhesus macaques (*M. mulatta*, Pomerantz & Baker, 2017; Symons, 1974). Research that demonstrated that macaques are aware of and sensitive to human gaze dates back to the 1960s (e.g. Wada, 1961) and research on macaques and tourism listed eye contact as a potential cause of primate aggression towards humans (Fuentes & Gamerl, 2005; Beisner et al., 2015). Our data on eye contact suggest that the macaques at Sepilok exhibit the same tendency to view human behaviours that closely resemble macaque aggression as threatening (Beisner et al., 2015; Berman et al., 2014; Fuentes & Gamerl, 2005; Ruesto et al., 2010). A minority of tour guides at Sepilok advised their guests to maintain a safe distance from the monkeys and to avoid direct eye contact, but visitors frequently ignored this advice. Other visitors did not receive this advice at all, either because their guide did not mention it or because they were travelling without one.

The presence of human food appears to be a strong and frequent contributing factor in rates of primate aggression towards humans at low-to-moderate staff intervention sites, such as those in Bali or Singapore (Fuentes & Gamerl, 2005; Sha et al., 2009). Unlike like those locations, neither food nor food cues were associated with aggression at Sepilok. In fact, interactions that involved food were so rare that they constituted only 2% of the total observed number of human-macaque encounters (0.03 bouts per hour). Similar results have been reported by Riley and Wade (2015), who found low rates of provisioning and

aggression among wild-living rhesus macaques in Silver Spring State Park, Florida. Beisner et al. (2015) found that provisioning of rhesus macaques in India was not associated with increased rates of aggression; in fact, within five minutes of provisioning, aggressive behaviour appeared to decrease. On the other hand, taunting (offering food and then pulling it away) was strongly associated with primate aggression towards humans (Beisner et al., 2015). Tourists offering food to macaques or having it stolen was significantly associated with primate aggression towards humans at Padangtegal, Bali and Singapore, although the authors did not specify whether taunting was included in those results (Fuentes et al., 2008; Fuentes & Gamerl, 2005; Sha et al., 2009).

Routine staff provisioning alone did not appear to cause aggression towards tourists or conspecifics in Tibetan macaques (*M. thibetana*) at Mt. Huangshan, China. However, maintaining the same levels of provisioning while also restricting the group's home range (i.e. corralling) likely caused increased feeding competition, and, by extension, inflated rates of intra-group aggression and infanticide (Ruesto et al., 2010). This corralling behaviour might explain why tourists throwing objects (e.g., tissues, rocks) at the macaques approached statistical significance in its association with primate aggression towards humans. At Sepilok, people never threw items at the macaques, which arguably reflects the positive effect that staff supervision and limiting tourists' belongings (i.e. high staff intervention) can have on tourist-macaque interactions.

While small amounts of food may increase intra-group aggression (Maréchal et al., 2016), a larger abundance of provisioned food within small macaque groups could serve to reduce intra-group conflict and, by extension, redirected aggression (Balasubramanian, Dunayer, Gilhooly, Rosenfield, & Berman, 2014). This trend in feeding competition may

help explain the relatively low rate of macaque aggression directed towards tourists at Sepilok given that the macaques can feed on orang-utan and bear provisions irrespective of visitor attendance.

The lack of bite and scratch wounds at Sepilok has important implications for the visitor experience by reducing the risk of injury and infection. Without open wounds, the risk of the transmission of zoonoses such simian foamy virus is greatly diminished (Schillaci et al., 2005). Fewer instances of close proximity also reduces the risk of primates contracting aerosol-borne human diseases such as measles and influenza, which can be fatal (Jones-Engel et al., 2001; Woodford, Butynski, & Karesh, 2002). These findings suggest that high staff intervention in the form of restricting visitors' access to food can have tangible effects on reducing the risk of aggression and, by extension, disease transmission at the human-macaque interface. These findings support what has been suggested by other researchers working on macaque tourism, i.e., that eliminating food should reduce aggressive encounters (Mallapur, 2013; Sha et al., 2009).

The ability to anticipate which human behaviours may cause macaque aggression will allow us to better mitigate undesirable tourist behaviour, which will benefit primates living within nature-based tourism sites while also teaching tourists appropriate behaviour for future encounters with wildlife. It is essential that we measure the effects of specific tourist intervention strategies in order to tailor recommendations for relevant primate species, tourism styles, and cultural and environmental contexts (see Riley & Wade, 2016). The measures of success will differ for each site depending, for example, on whether rehabilitation is a part of the site's mandate, the geographic layout of a location, the behaviour and past experiences of the resident primates, and the expectations of the

tourists. Understanding these conflicting desires along with the biological reality of disease transmission and the financial costs of expanding educational programs is essential in order to make effective, practical changes to tourist sites. Any changes to education programs or tourist guidelines will need to be made through collaboration with local site personnel given that they are typically the ones best situated to understand the potential impacts of changes to site policies (Muehlenbein & Wallis, 2014). The results of this study demonstrate that reducing tourists' access to food while also educating them on the importance of avoiding eye contact with macaques can significantly reduce the risk of physical aggression. Ideally, effective tourist management strategies that are based on specific behavioural patterns will have positive effects beyond reducing the frequency of one or two unwanted behaviours.

4.5 References

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Chapter Five

5 The Effects of Routine Provisioning and Proximity to Tourists on Macaque Feeding and Ranging Patterns

5.1 Introduction

Primate populations are in decline world-wide because of deforestation, with the added pressure of hunting, the pet trade, emerging infectious disease likewise contributing to their demise (Estrada et al., 2017). Infectious disease in particular has received a considerable amount of attention in the research literature due to its potential to cause sudden and devastating mortality amongst wild primate groups (Wallis & Lee, 1999). An ecological approach to infectious disease requires a broad understanding of the ways that environmental and evolutionary forces can affect parasite dynamics both within and between species. A recent focus on changing patterns of parasite exposure and transmission in primate species has called for interdisciplinary methods that draw from anthropology, ecology, evolutionary genetics, and epidemiology (Balasubramaniam et al., 2019).

A holistic approach to the conservation of wild primates involves understanding the multiple (if occasionally contradictory) effects of anthropogenic activities and infrastructure on primate health. This task becomes more complicated as more primary forest is degraded or cleared, creating edge effects that can alter the local micro climate, species composition, and resource availability (Patz et al., 2004; Qie et al., 2017). Edge effects have long been associated with an increase in *spillover* events, where pathogens move between wildlife to domestic animals or humans. The risk for such events appears highest when intermediate levels of land conversion create an edge that is densely

populated on both sides, e.g. human settlements and livestock on one side of the edge, and numerous faunal communities within the adjacent forest (Faust et al., 2018). Given this risk, macaques (*Macaca* spp.) are a particularly important taxa to consider in the epidemiology of forest edges because their generalist nature allows them to thrive in a number of different anthropogenic environments (Balasubramaniam, Sueur, Huffman, & MacIntosh, 2019). They may be among the main attractions at a location where they are hand-fed human food by tourists (Grossberg, Treves, & Naughton-Treves, 2003), or they may simply occupy an area that tourists visit to see cultural landmarks or other wild or rehabilitating animals, as is the case in the current study.

Infectious disease spread by humans is often cited as the most pressing issue threatening primate health at tourism locations and is be described as a uniformly negative consequence of tourism (Muehlenbein & Anrenaz, 2009; Wallis & Lee, 1999). However, not all potential side-effects of tourism are quite as absolute. The same provisioning that might expose primates to harmful contaminants may also provide nutrient-rich food, thus potentially improving immune function, increasing fecundity, and providing a buffer against the harmful effects of infectious disease (Fuentes et al., 2011). Likewise, a decrease in time spent foraging should also limit exposure to infective-stage helminths (Lane, Holley, Hollocher, & Fuentes, 2011). While a change in home range size or strata use should not affect the transmission of parasites that are spread within a group via direct contact (e.g. ectoparasites), shifts in a group's home range from forest to an anthropogenically-modified environment could reduce the amount of exposure to free-living environmental parasites (Walther, Clayton, & Gregory, 1999; Wenz et al., 2010).

Understanding the effect of habitat use on the risk of parasite exposure in primates requires knowledge of typical home range size, seasonal variation, vegetation quality and abundance, social dynamics, and various other biological and environmental factors (Balasubramaniam et al., 2019; Chapman, Gillespie, & Goldberg, 2005; Patz et al., 2004). However, we can generally apply the rule that larger home ranges should result in an increased exposure to parasites and a concomitant rise in species richness within a primate group (Garrido-Olvera et al. 2012; Gregory 1990). However, considerable variation in the habitat characteristics within a primate's home range complicate this hypothesis. While external factors such as temperature, rainfall, and tree fruiting patterns may affect feeding and ranging patterns, it is crucial that researchers examine fluctuations in anthropogenic activity that may affect primate foraging strategies (Klegarth, 2016).

It is possible that the consistent availability of nutrient-dense food may counteract the negative implications of tourism for primates in a highly controlled environment, such as rehabilitation centers. Our study site featured a constant supply of provisioned food year-round for rehabilitating orang-utans and sun bears that was fed on opportunistically by the study group of macaques. This made it an appropriate location to address the following research questions: i) how does provisioned food affect the activity patterns of wild macaques at a popular tourist site? ii) does the group's proximity to tourist infrastructure fluctuate based on time of day or levels of visitor attendance? and iii) how does home range change throughout the year in relation to tourist activity? Since the study group was comprised of long-tailed macaques (*Macaca fascicularis*), pig-tailed macaques (*M. nemestrina*) and their hybrid offspring, we also sought to provide basic demographic data on group social structure.

5.2 *Methods*

5.2.1 *Tracking data*

We collected GPS data points every 15 minutes from the approximate center of the group in order to track their movement throughout the day. Since none of the animals were fixed with a GPS collar, data points had to be taken manually during full-day follows. There were enough breaks in the forest canopy throughout the home range to allow for fairly accurate satellite detection, therefore the GPS error was typically between 5 and 7 m. Very few data points were missed due to a location error of 10 m or more (McKinney, 2011).

GPS data collection began at approximately 0700h and continued until we either lost the group or until the alpha male climbed to his roosting site at dusk, typically around 1745h. If we did not know where the group was (either because we had lost them the previous day or because we did not know where they slept the night before), we searched for them and began both behavioural and GPS data collection as soon as we found them. In the interest of safety, we avoided following the group during periods of heavy rainfall. Thus, the GPS data collection is biased towards behaviour during little to no rain. However, the group typically did not move during periods of heavy rain.

5.2.2 *Behavioural Data Collection*

We conducted 10-minute focal follows on a total of 15 individuals from 0800h – 1600h during full-day tracking. We began behavioural data collection at 0800h because that was when we could be sure that all members of the group would have descended from their sleeping tree, thus avoiding biasing the morning data collection towards the individuals that

consistently woke up earlier than the others. Likewise, we terminated data collection at 1600h to ensure that variation in the timing of the groups' roosting behaviour did not skew the distribution of the focal follow sessions.

Focal follows were divided into four 2-hour blocks (0800-1000, 1000-1200, 1200-1400, 1400-1600), and we attempted to follow an individual only once during each block. We tried to ensure that data collection was even across all individuals of the group, but this was difficult for those that spent more time on the periphery of the group, especially because we needed to balance the need for behavioural data with the need for observing interactions between the group and tourists. We recorded a minimum of three behavioural variables every minute, and a maximum of four other variables were recorded if they were relevant (Table 5.1).

We allowed for one out-of-sight data point for each focal session. If an individual was out of sight for two or more data points, that session was abandoned. We did not start a follow session if the individual was partially obstructed such that we could not be sure of their behaviour, e.g. whether they were grooming or eating.

TABLE 5.1. Ethogram of behaviours recorded during 10-minute focal follow sessions.

Variable	Mandatory	Options	Definition
Strata	Yes	boardwalk	Wood or metal surface used by tourists.
		ground	Forest floor, grass, or stream.
		other	Man-made structures, e.g. fence, roof, rope, road.
		platform	Feeding platform used by orang-utans.
		railing	Hand railing used by tourists at SORC and BSBCC.
		tree	'Natural' structure above ground, e.g. tree roots.
Activity	Yes	eat	Manipulating or consuming food or food packaging.
		rest	Sitting or lying down without engaging in feeding or social behaviour.
		social	Grooming or being groomed.
		travel	Walking, running, or jumping on any surface.
Food source	If relevant	crop	Fruit or vegetables that came from a garden, e.g. banana
		human	Food or packaging from tourists, e.g. water bottle
		orang-utan	Provisions intended for the orang-utan feedings.
		sun bear	Provisions intended for the sun bears.
		wild	Food that was not obtained from either staff or tourists.
Food type	If known	invertebrate	Insects
		flower	
		fruit	
		young leaf	
		stem	
		vertebrate	Mouse, colugo.

5.2.3 Home Range Use

There are a number of methods that can estimate the home range of primate groups that do not rely on intensive data collection through satellite collars (Stark et al., 2017). Minimum convex polygons (MCP) are straightforward to create, but they typically overestimate home

range while obfuscating areas of intense use (Amaral Nascimento, Schmidlin, Valladares-Padua, Matushima, & Verdade, 2011). Conversely, the grid cell method can better illustrate the intensity of a group's movement throughout a home range, but it lacks specificity in illustrating daily or monthly variation (Grueter, Ren, & Wei, 2009). Kernel utilization distributions (KUD) are also effective tools for estimating home range size and illustrating intensity of use. They are frequently used in lieu of more complex time-based methods that rely on regular, high-frequency spatial data, which is generally achieved through satellite tagging (Benhamou & Cornélis, 2010; Kie et al., 2010).

A 95% kernel utilization distribution (KUD) map was carried out in R (version 3.5.0) using package *adehabitatHR* (Calenge, 2006). Smoothing parameters were chosen using the function *href*, which generates a bandwidth based on the variation of the GPS data. We chose this automated method because the alternative, least square cross validation, is not ideal for large sample sizes (Hemson et al., 2005). Data points were assigned one of three categories: peak visiting hours (1000-1200h, 1500-1600h), off-peak visiting hours (0900-1000h, 1200-1500h, 1600-1700h), and closed (0700-0900h, 1700-1800h).

Using the buffer tool in QGIS (version 2.18.2), I created a 10 m wide buffer zone around the buildings, walkways, and parking lot used by visitors at both the SORC and BSBCC in order to generate a single tourist area polygon (Figure 5.1). We selected this distance because it reflected common best practices in ecotourism, where visitors are often encouraged to stay 10 m or more away from wild primates (Gilardi et al., 2015). Therefore, if the macaques were located within the 10 m buffer, they could be within 10 m of a tourist.

We measured the shortest Euclidean distance between each GPS point and the tourist buffer and a Kruskal Wallis rank sum test was used to compare the median distance

to the tourist buffer for each of the three time periods. A 95% kernel utilization distribution was then used to measure the home range size for each time period, which also acted as a better illustration of the group's intensity of home range use.

We used the *vector grid* function in QGIS to conduct a grid cell analysis of the group's home range (Stark et al., 2017). We used a 50 x 50 m grid following the methods of Hoffman & O'Riain (2011) where the cells were large enough to include the entire group at one time. The GPS points within each square were counted using the *points in polygons* function in QGIS and classified into nine categories based on the total number of points per cell (see Figure 5.2).

Neither MCPs, GCMs, or KUDs are designed to identify physical boundaries, such as cliffs or rivers, within a home range (Benhamou & Cornélis, 2010; Powell, 2000; Stark et al., 2017). However, for the purposes of this study, we were more interested in assessing the intensity of home range use as well as the proximity of the study group to the tourist area rather than overall home range size. We used a 95% KUD to compare the relative home range size when grouped by visiting hours, while the GCM method allowed us to identify areas that the macaques used frequently.

5.2.4 Statistical Analysis

Spearman's rank tests were used to explore the monotonic relationship between the number of tourists per day and i) mean distance from the tourist buffer and ii) distance to sleeping sites. We also used a binomial general linear model (GLM) with a logit link in R (version 3.5.0) to explore the effects of both time of day and daily tourist attendance on macaque movement. The dependent variable was scored as either in or out of the tourist buffer zone.

We included daily tourist numbers and opening times as a factor (closed, off-peak, peak times), and an interaction term between numbers and opening times as explanatory variables. We used a stepwise model reduction to remove any non-significant explanatory variables using the “drop1” function. Prediction graphs were generated from the resulting final model using the package *effects* and visualized using the package *ggplot2* (Fox, 2003; Wickham, 2016).

5.3 Results

5.3.1 Group Composition

The Sepilok macaques did not appear to use the ‘multi-level’ structures proposed by Caldecott (1986) and Robertson (1986). That is, they slept, travelled, and ate as one cohesive unit. The only exception to this was the transient nature of one of the adult long-tailed macaque males, who was not present every day (Table 5.2).

TABLE 5.2. Demographic profile of the hybrid macaque group.

Age Category	Sex	Species	Number in Group	
			Nov. 2016	Aug. 2017
Adult	Female	Pig-tailed Macaque	4	3 [†]
		Long-tailed Macaque	1	1
		Hybrid	2	2
	Male	Pig-tailed Macaque	3	3
		Long-tailed Macaque	2	1 [‡]
		Hybrid	0	0
Immatures	Combined	Pig-tailed Macaque	5	8
		Long-tailed Macaque	2	2
		Hybrid	2	3 [§]
Total:			21	23
[†] 1 individual was missing and presumed dead in December, 2016. [‡] 1 individual emigrated in July, 2017. [§] Infant born to 2 nd generation hybrid in July 2017 and died in August 2017. One other hybrid infant survived.				

5.3.2 Movement

The tourist buffer measured 0.04km² and contained 20.2% of all GPS data points (N=4699). The points inside the tourist buffer ($n=949$) were not evenly distributed between closed (30.2%), off-peak (46.6%), and peak visiting hours (23.2%). A Pearson's chi-square test revealed that the number of GPS points within the tourist buffer across all three time periods was significantly higher than expected by chance ($p<0.001$).

There was considerable variation in tourist attendance throughout the year. The orang-utan center received approximately 9979 visitors per month (Standard deviation: 2610; minimum: 6466; maximum: 14051). The sun bear center, on the other hand, received approximately 5978 visitors per month (Standard deviation: 1746; minimum: 3401; maximum: 9140). There was no correlation between daily visitor attendance and the daily distance of the macaques from the tourist buffer (Spearman's rank: $p=0.78$) or distance to the macaques' sleeping site (Spearman's rank: $p=0.25$). The Kruskal-Wallis test revealed that there was a significant difference in the median distance from the group to the tourist buffer during the three different time periods throughout the day ($p<0.001$). A post hoc Dunn test showed a significant difference between the median distance during peak visiting hours (46m) compared to closed (36m, $p<0.001$) and off-peak (38m, $p<0.001$).

The KUD analysis suggests that the macaques were more clustered around the tourist area during closed hours compared to peak and off-peak (Figure 5.1). Similarly, the GCM map illustrates that several of the cells visited the most frequently by the group included the feeding platforms and overlapped with the tourist buffer. After stepwise deletion using the *drop1* function, tourist numbers and opening times were left as significant explanatory variables.

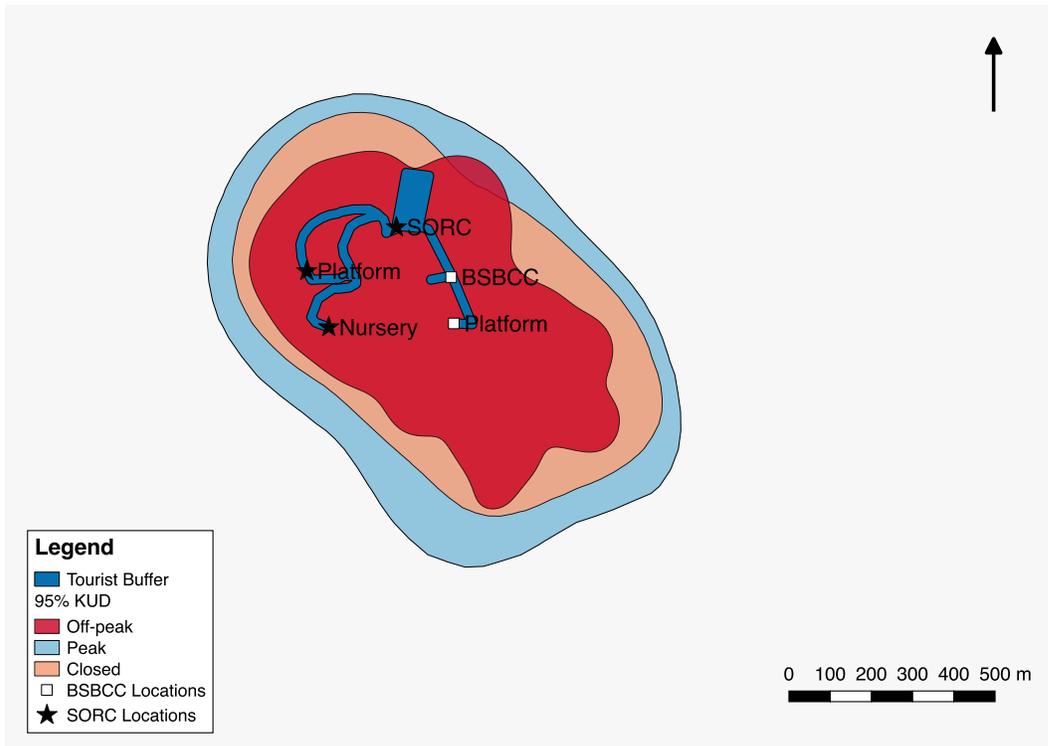


FIGURE 5.1. 95% kernel utilization distribution for the three time periods. The median distance to the tourist buffer was highest during the peak visiting hours.

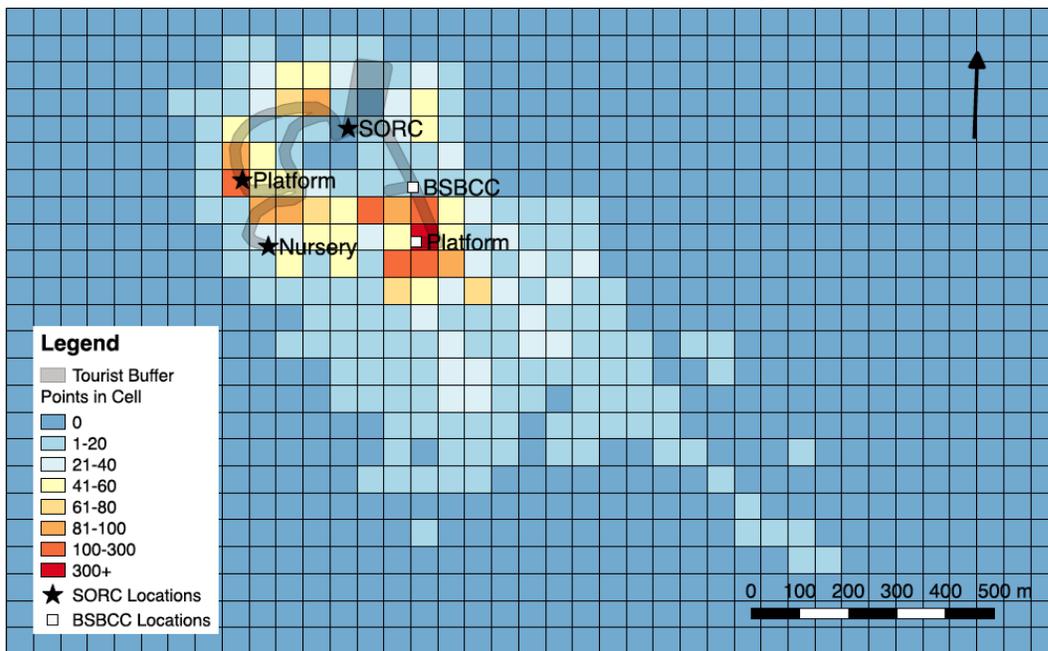


FIGURE 5.2. Grid cell map illustrating the intensity of home range use near the tourist buffer.

The number of tourists attending the rehabilitation centers appears to have a slight effect on the group's movement, where the probability of the group being found outside the tourist buffer increased by 0.03% for every tourist added to the binomial general linear model (Figure 5.4; Residual deviance = 4777.0 on 4695 degrees of freedom; Null deviance = 4822.8 on 4698 degrees of freedom).

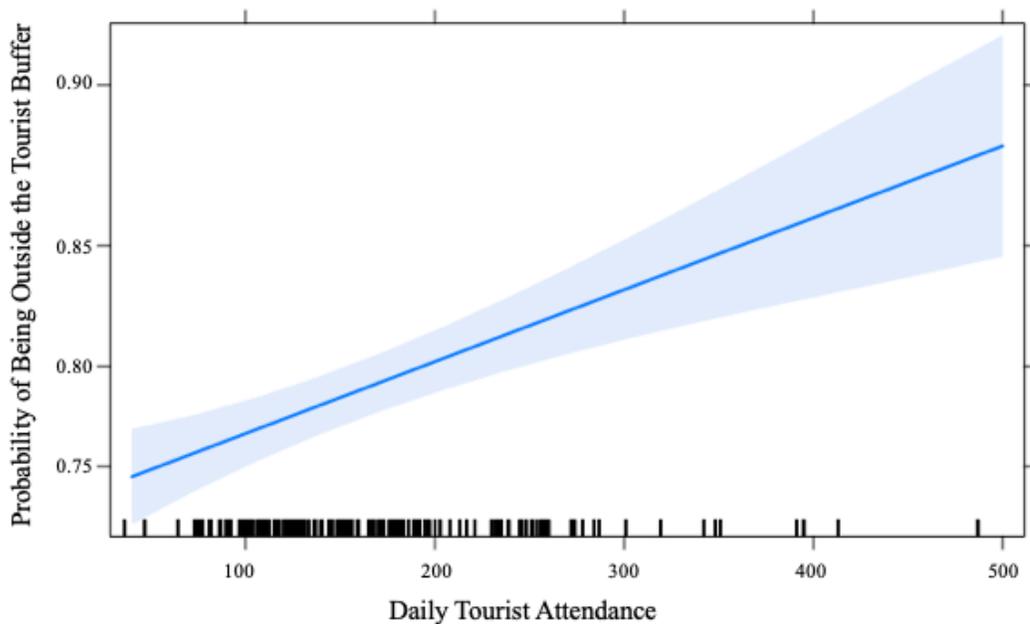


FIGURE 5.3. Prediction graph showing the probability of the macaques being found outside the tourist buffer based on visitor attendance.

5.3.3 Feeding Behaviour

Combined orang-utan and sun bear provisions accounted for approximately 34% of the observed feeding bouts per month (standard deviation = 7.7; range: 22-51). There was a negative correlation between the proportion of time spent eating compared to time spent sleeping ($Rho = -0.468$, $S = 657200$, $p < 0.001$). The GLM revealed a significant positive relationship between the proportion of provisioned food and time spent resting (Figure 5.4), with a stronger effect when the proportion of provisioned food was higher.

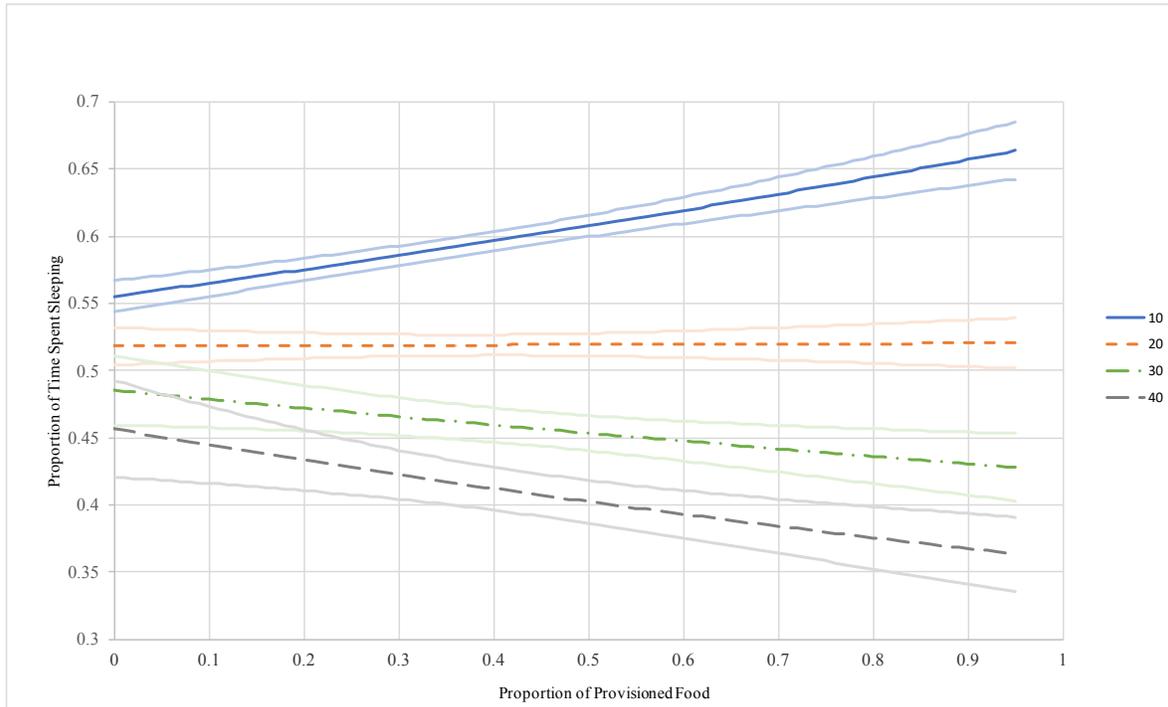


FIGURE 5.4 – Predictions of time spent sleeping (including standard error) in relation to proportion of provisioned food. Provisioned food is predicted as a per cent of daily feeding bout observations..

5.4 Discussion

5.4.1 Feeding Behaviour

The Sepilok macaques relied on orang-utan and sun bear provisions during approximately one-third of observed feeding bouts during the 10-month study period. They also spent more time resting when they consumed higher levels of provisioned food, and this relationship changed depending on the proportion of provisioned versus non-provisioned feeding bouts. These results are in line with research on primates where proximity to human-modified sites was associated with changes in feeding behaviour (Altman & Muruthi, 1988; Fuentes et al., 2011; Lane et al., 2010; Wenz-Mücke et al., 2013). These

results are important to the discussion of tourism and primate well-being because changes in feeding patterns may have effects beyond a simple decrease in time spent foraging.

There is a precedent for a positive association between access to human provisions and infant survival rate (Fuentes et al., 2011) as well as time spent on the ground in wild macaques (Wenz-Mücke et al., 2013). Given the risk of exposure to environmental helminths living in soil, these results beg the question of how to weigh the benefits of access to nutrient-rich food against potential exposure to infection. In addition to increased fecundity, long-tailed macaques throughout Bali appear to benefit from their proximity to popular tourist sites through reduced parasite prevalence and intensity as well as an increased amount of time spent resting (Fuentes et al., 2011; Lane et al., 2010; Lane et al., 2011). The same can be said for baboons (*Papio* sp.) living in close proximity to anthropogenic environments who experienced a significant decrease in helminth burden (Weyher, 2009) and home range size (Altman & Muruthi, 1988). Further long-term data are needed to elucidate the effects of provisioning on infant survival within the Sepilok macaques. However, every adult female in the Sepilok study group gave birth during the study period. All but one—who was believed to be nulliparous at the beginning of the study—also had a surviving yearling at the time of their most recent birth. The macaques also did not show any obvious signs of obesity, which can have negative implications for overall health (McCurdy et al., 2016). Much like the long-tailed macaques of Bali, the frequency of provisioning in a complex anthropogenic environment appears to confer an advantage to the Sepilok macaques (Fuentes et al., 2011; Lane et al., 2011).

This potential effect on home range size and time spent on the ground could be important because differences in strata use may have implications for species-specific patterns in disease prevalence. Blood parasites, for example, frequently make use of biting flies as vectors, which are more abundant in the upper canopy compared to the understory. Therefore, host species that spend more time in the upper canopy may experience greater blood parasite prevalence (Garvin & Remsen, 1997). Meanwhile, time spent in the understory could result in greater exposure to ticks and mosquitoes, who typically find hosts closer to the ground (Brant et al., 2016; Pruett-Jones, Pruett-Jones, & Jones 1991). The study at Sepilok somewhat muddles discussions of strata-related exposure given that not all individuals within the group move through their home range in the same way (chapter 6, this volume). Since pig-tailed macaques were more likely to be on the ground compared to long-tailed macaques, a shift in the proportion of time spent on anthropogenic structures, such as railings, may affect pig-tailed macaques more significantly through reducing their exposure to free-living parasites in soil.

This study group further benefits from their proximity to Sepilok given that they are not exposed to some of the potential sources of parasites found in disturbed habitats, such as standing pools of water, domestic animals, and human waste (Barth et al., 2017; Weyher, 2009). A key caveat to the hypothesis that tourism may be beneficial for generalist species such as macaque and baboons is that nutritional benefits should be coupled with a low likelihood of physical contact and intense human-directed aggression, which would increase the risk of anthrozoonotic disease transmission via bodily fluids and aerosol vapors. The provisions at Sepilok can be accessed easily and require little handling time (Schoener, 1971), which means that macaques appear to experience high nutritional

benefits without the elevated rates of direct contact and related infectious disease risk seen at other popular tourist sites throughout Asia. Further investigation into the parasite ecology of these macaques may help determine whether consistent use of anthropogenic structures amplifies the potential mitigating effect of provisioning on parasite exposure and acquisition.

5.4.2 Macaque Movement

The KUD demonstrated that the study group's home range included the entirety of the SORC and BSBC, with the exception of the main entrance and canteen area. The median distance to the tourist buffer appeared to be significantly higher during the closed time period. However, this slightly increased distance was less than would be expected if the group was attempting to avoid visitors entirely. Instead, an increase of 10 m compared to the closed period and 8 m compared the off-peak period suggests a minor attempt to avoid the tourist area. Given that the daily tourist attendance had a minimal effect on the group's proximity, it is possible that this trend towards a slight avoidance during peak visiting hours is a by-product of unrelated behaviour, including sleeping site preference and wild foraging patterns.

These slight but significant patterns complemented our observations of the macaques when they were approached by tourists. We occasionally observed individual macaques move out of the way for tourists, but the group as a whole was never displaced by visitors (Gilhooly, unpublished data). Crucially, the macaques did not engage in avoidance behaviour as defined by Williamson and Feistner (2003) whereby primates will retreat quickly and silently to avoid people.

The KUD analysis illustrates how intensely the macaques used the tourist buffer area, where a mere 9% of their home range accounted for 20% of the GPS data across all time periods (see Figure 5.1). The KUD analysis also illustrates that the tourist buffer was fully encompassed by the polygon illustrating all three of the different time periods: closed, off-peak, and peak. Likewise, the grid cell analysis identified two areas of intense use within the group's home range, both of which were near the orang-utan and sun bear feeding platforms (Figure 5.2). While this might appear to contradict the results of the Kruskal-Wallis and KUD analyses, the frequent use of the sun bear center as a sleeping site likely contributed to the significant clustering of GPS points around the feeding areas during closed hours.

In general, the study group neither drastically avoided the tourist area nor did they seek close contact with tourists (Chapter 4, this volume). They appeared to move through their home range unencumbered by the activity of humans around them while spending a considerable amount of time near both feeding platforms. This lack of major avoidance behaviour combined with the absence of intense aggression is an encouraging example of a synecological existence between tourists and wild primates when provisioning is conducted by trained professionals.

5.5 *Conclusions*

The lack of provisioning by tourists at Sepilok likely contributed to the slight avoidance by the macaques of tourist-dense areas during peak visiting hours. These results are reassuring because they demonstrate that macaques do not appear to seek out experiences with tourists when there is no nutritional incentive to do so. However, the spatial analyses demonstrated

that the macaques still spent a considerable amount of time near the tourist area, which may have an effect on their exposure to free-living parasites in the environment.

The association between provisioned food and time spent resting supports previous studies that demonstrated the effect of proximity to human settlements on the feeding and ranging behaviour of wild primates. Understanding the effects of tourism, then, becomes increasingly important when proximity to a tourist site can provide considerable health benefits for generalist species, such as macaques. The on-going association between macaques and human settlements at forest edges, including nature-based tourism sites, makes it unlikely that wild macaque groups can be completely deterred from using anthropogenic environments. Efforts to reduce conflict between macaques and tourists are perhaps best spent on how to limit direct contact rather than attempting to keep both species entirely separate.

5.6 References

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6 Parasite Prevalence and Species Richness in a Hybrid Macaque Group

6.1 Introduction

6.1.1 Primates and Parasites

As emerging and re-emerging infectious diseases have gained prominence as public health risks amongst humans, increasing habitat fragmentation and land conversion have continued to jeopardize biodiversity worldwide (Estrada et al., 2017; Patz et al., 2003). For decades, the transmission of viruses, bacteria, and protozoa from humans (i.e. anthroozoonotic diseases) has been a well-known threat to wild primates in particular. Now, however, the potential for humans to influence free-living parasite (i.e. helminth) prevalence through either direct transmission or through changes to primate feeding, ranging, or dispersal behaviour is garnering more attention because of the wide-ranging conservation implications of helminth infection (Balaubramaniam, Sueur, Huffman, & MacIntosh, 2019; Lane-deGraaf et al., 2010; Wenz-Mücke, Sithithaworn, Petney, & Taraschewski, 2013).

Some pathogens, such as the influenza virus, are capable of infecting distantly related species, including mammals and birds (Zanin et al., 2017). In cases of such phylogenetically diverse hosts, geographical overlap and shared ecological niches become the most important predictors of disease transmission (Cooper, Griffin, Franz, Omotayo, & Nunn, 2012; Davies & Pedersen 2008; Locatelli & Peeters, 2012). Helminths, on the other hand, tend to be more species-specific regarding potential hosts. Therefore, phylogenetic distance becomes the most important predictor of pathogen sharing, with the probability of crossover increasing with a decrease in phylogenetic

distance between species (Engelstädter & Fortuna, 2019; Park et al., 2018; Wolfe, Dunavan, & Diamond, 2007). The study of helminths in primates is therefore relevant to both conservation and public health issues due to the shared evolutionary history with humans, the frequency with which humans and primates interact, and the subsequent risk for cross-species disease transmission as human land use changes continue to encroach on primate habitats (Fountain-Jones et al., 2018; Kim, Coble, Salyards, & Habing, 2018; Muehlenbein & Wallis, 2014).

Helminth species richness tends to correlate positively with host species richness within distinct habitat patches (Kamiya, O'Dwyer, Nakagawa, & Poulin, 2014; Poulin, 2014). It stands to reason, then, that increased overlap between primates and humans due to land-use patterns and associated changes in the home range of primates will increase the risk of wild primates encountering new parasites, or encountering parasites to which they have already been exposed at higher rates (Frias et al., 2018b; Lane, Holley, Hollocher, & Fuentes, 2011; Loudon & Sauter, 2013; Weyher, 2009). Even in the absence of humans, overcrowding as a result of ongoing anthropogenic habitat disturbance and fragmentation may cause more contact within and between non-human primate species, which may further facilitate parasite transmission (Anderson & May, 1992; Chapman, Gillespie, & Goldberg, 2005; Lane et al., 2011; Wenz, Heymann, Petney, & Taraschewski, 2010).

While parasites are ubiquitous in ecological systems, an individual that carries one or more intestinal parasites may not necessarily experience significant illness (Chapman, Gillespie, & Goldberg, 2005; Weyher, 2009). However, heightened exposure to parasites caused by human alteration of habitats could result in an increased risk for adverse health effects in wild primates, including compromised immune function and

spontaneous abortion (Agostini, Vanderhoeven, Di Bitetti, & Beldomenico, 2017; Hussain, Ram, Kumar, Shivaji, & Umapathy, 2013; Lane et al., 2011). Research on helminths in primates is buoyed by the fact that faeces can be collected non-invasively and examined *in situ* with fewer resources compared to other techniques (but see below). As a multidimensional problem, patterns of emerging infectious disease require multidisciplinary solutions. In order to predict changes in parasite-related morbidity, the impact of humans and anthropogenic land changes on parasite avoidance and acquisition behaviour in primates must be understood (MacIntosh, 2014; Wenz-Mücke et al., 2013).

6.2 Research Questions

The purpose of this chapter is to provide a preliminary glimpse of the parasite species richness (PSR) of a naturally-occurring hybrid group of macaques (*Macaca fascicularis*, *M. nemestrina*, and their hybrid offspring). We also highlight some of the next steps in parasitological analyses of enigmatic primate populations. Specifically, the following questions will be addressed: i) what parasite types are present in the study group? ii) what are the mean eggs per gram (EPG) values for each type of parasite? iii) do EPG values differ between age, sex, or species categories?, and iv) does strata use differ between age or species categories? This chapter also outlines many of the questions that were raised by these preliminary results and identify potential next steps to address the current gaps in our knowledge.

6.3 Materials and Methods

6.3.1 Study Species

Fresh faecal samples were collected from a hybrid group of wild macaques living within the Kabili-Sepilok Forest Reserve. Group size ranged from 21-23 individuals during data collection, including 4 true long-tailed macaques (LTM), 14 true pig-tailed macaques (PTM), and 5 suspected hybrid macaques. Hybridity was assessed based on staff knowledge of group history and morphological characteristics. Genetic data are pending.

6.3.2 Study Site

This site represents a unique opportunity to study the parasite ecology of a group of macaques that feed in part on provisioned fruit and vegetables but who experience low rates of direct contact with humans. Data collection took place at the Sepilok Orang-utan Rehabilitation Center (SORC) and the adjacent Bornean Sun Bear Conservation Center (BSBCC), which are located on the perimeter of the Kabili-Sepilok Forest Reserve. The reserve is approximately 55km² and the area that comprises the macaques' range consists of lowland dipterocarp and heath forest (Liu et al., 2018). Both the orang-utans and the sun bears are provisioned twice daily with a combination of local fruit and vegetables.

Screening the orang-utans and sun bears at the rehabilitation centers for parasites was beyond the scope of this study, but these co-habitants within the reserve represent a potential future line of inquiry in order to assess the risk of cross-species disease transmission. The other primate species in the reserve are the red langur (*Presbytis rubicunda*), Philippine slow loris (*Nycticebus menagensis*), Horsfield's tarsier (*Cephalopachus bakanus*), and the northern gray gibbon (*Hylobates funereus*). The study group was never observed interacting with any of these species.

6.3.3 Behavioural Data

For the purposes of this chapter, strata use is divided into ‘ground’, which includes terrestrial contexts, such as soil, mud, water, or grass, and ‘other’, including trees, roots, fences, roofs, railings, and feeding platforms. Concrete was also included as ‘other’ because it is not likely to host environmental parasites the same way soil would (Ziemer et al., 2010). Strata use was recorded every minute for 10 minutes during individual focal follows for a total of 66,331 data points between 15 focal individuals. The daily proportion of ‘ground’ to ‘other’ was calculated for each focal animal in order to compare species and age patterns in strata use.

6.3.4 Faecal Collection

We collected 232 faecal samples from 15 different monkeys from November 2016-August 2017 (Appendix 1). Samples were collected opportunistically and stored them in sodium-acetate-formalin (SAF) fixative in a 1:3 ratio after thorough homogenization. SAF fixative was used because of its easy availability, the ability to be stored at room temperature, and its limited amount of dangerous chemicals, such as formaldehyde (see MacIntosh et al., 2010). We collected samples from the center of the faecal pellet, making sure to avoid matter that was touching the soil or that had been contaminated with urine. A faecal sedimentation method was used to identify helminths to the genus level based on egg morphology (Greiner & McIntosh, 2009; Hasegawa 2009).

Faecal processing was carried out by the author at the Danau Girang Field Center, located within the Lower Kinabatangan Wildlife Sanctuary in eastern Sabah.

Approximately 10 ml of faecal-SAF solution was agitated and strained through two

layers of gauze and washed with saline solution until a total of 14 ml was reached. This solution was centrifuged at 3000 rpm for five minutes, after which the supernatant was discarded, and the sample was weighed. The weight of the pellet was calculated by subtracting the weight of the dry tube from the total weight of the sample. The remaining pellet was resuspended in 8 ml of saline solution and 4 ml of ethyl acetate, shaken vigorously for 30 seconds, and subsequently centrifuged at 3000 rpm for five minutes. The separated faecal plug was gently loosened from the walls of the tube and discarded along with the supernatant. The remaining concentrated faecal pellet was resuspended in 3 ml of SAF fixative, divided into 1 ml aliquots, and stored for future microscopy.

1 ml aliquots were suspended in 10 ml saline for microscopic analysis. Four McMaster chambers were examined at 10x magnification for each sample, ensuring that the aliquot was homogenized thoroughly prior to each extraction. If the sample was not clear enough for examination, an additional 5 ml of saline was added. The mean value of the four chambers was used to calculate the EPG of faeces for each genus based on the weight of each sample after the first round of centrifugation and the total amount of saline used for examination.

We calculated overall PSR as the total number of genera identified across all of the recovered faecal samples. Z-scores were used to illustrate the differences in mean EPG between each individual over the entire study period relative to the sample mean. Z-scores were calculated using the following formula (Formula 6.1):

$$Z = \frac{(x - \bar{x})}{s}$$

Where x is the individual's mean EPG, \bar{x} represents the sample mean, and s represents the standard deviation of the sample mean. Calculating EPG is useful for quantifying the relative amount of each parasite taxonomic group carried by an individual. However, EPG cannot reliably be used to infer anything about the intensity of an infection (Gillespie, 2006). This is due in part to the fact that an increase in the expulsion of eggs could reflect a surge in immune function (MacIntosh, 2014). The relationship between infection and egg count is also confounded by the possibility that parasite burden could be mitigated by improved diet in higher-ranking individuals (MacIntosh, 2014; Muehlenbein et al., 2010). Therefore, we report EPG as a means of quantifying relative rates of infection, rather than empirical assessments of subjective symptoms of illness. In the case of *Balantidium* sp., we report cysts per gram (CPG).

Identifying distinct helminth species using morphology alone is highly precarious due to the sheer biodiversity of the phylum Nematoda and the morphological similarities between species, even at high magnifications (Hasegawa, 2009). For example, recent research on *Trichuris* sp. demonstrated that species identification without molecular methods was unreliable due to the extensive diversity within the genus (Cavellero et al., 2015). Therefore, we limit our identification of parasites to the genus level because of our lack of molecular data.

6.3.5 Statistical Analyses

Schapiro-Wilk tests of normality were conducted on the mean EPG for each parasite grouped by both age and sex and a Mann Whitney U test was used to test for significant differences between categories with respect to both PSR and EPG values. We used a Kruskal-Wallis chi-square test to explore differences between mean PSR and mean EPG

between the three species categories: long-tailed macaque, pig-tailed macaque, and hybrid. We also used a one-way ANOVA test because of its robust ability to handle violations of assumptions, including non-normal distributions of data. Strata use was compared between adults and juveniles and between species categories using a proportional binomial general linear model (GLM). We conducted all statistical tests using SPSS 25 (v. 25.0.0.0).

6.4 Results

6.4.1 Parasite Prevalence

We collected approximately 1.5 samples per monkey, per month and recovered at least four different groups of helminth (Appendix 6.1). Both *Balantidium sp.* and *Trichuris sp.* had a mean monthly prevalence of 0.92, followed by an unknown strongylid (0.83), and *Strongyloides sp.* (0.56). *Balantidium* resulted in the highest counts among all of the observed parasites, while the unknown strongylid had the highest EPG values of the helminths (see Table 6.1).

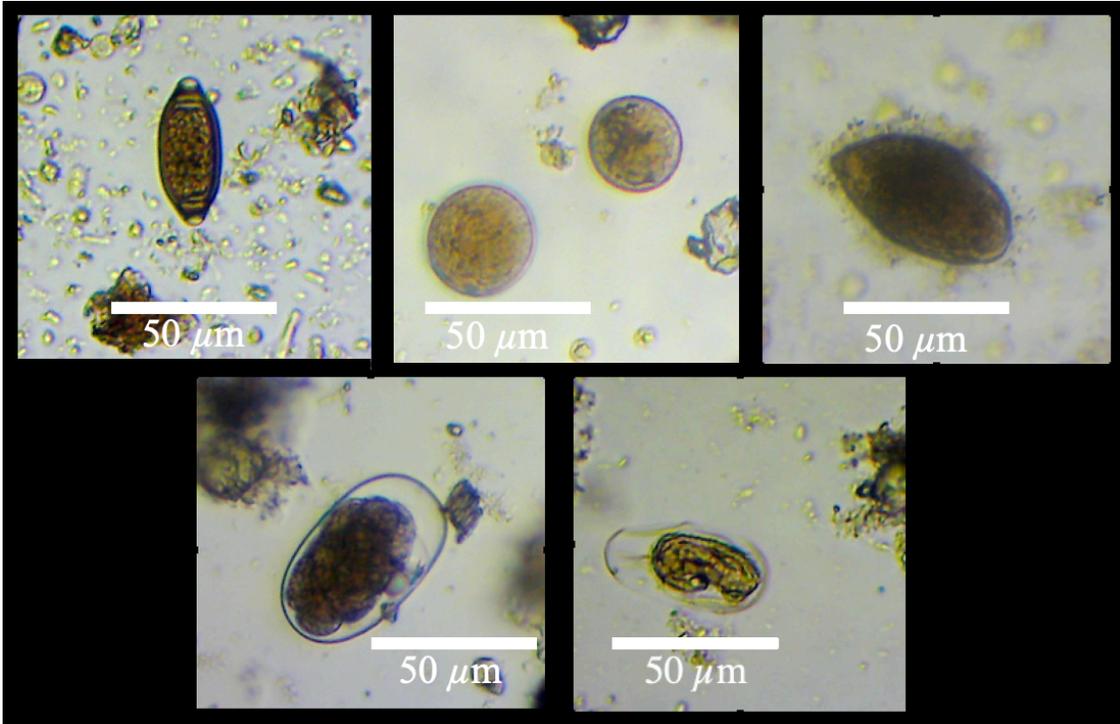


FIGURE 6.1. Four distinct parasite taxonomic groups included in the present analysis. Clockwise from top left: *Trichuris* sp., *Balantidium* sp. cyst, *Balantidium* sp. trophozoite, *Strongyloides* sp., unknown strongylid.

TABLE 6.1. Z-scores (number of standard deviations above or below the total mean) for each parasite based on the mean EPG for each monkey.

Monkey	Age	Sex	Species	<i>Trichuris</i>	<i>Balantidium</i> *	Unk. strongylid	<i>Strongyloides</i>
Bajung	Adult	Female	PTM	-0.6	0.1	-0.1	-0.9
Bruno	Adult	Male	LTM	-1.1	0.3	-0.7	-0.7
Bunga	Adult	Female	Hybrid	-1.0	2.2	-0.5	-0.7
Campur	Adult	Female	Hybrid	1.6	0.3	-0.1	-0.5
Charlie	Adult	Male	PTM	1.7	-1.1	-0.6	1.4
Coklat	Adult	Female	PTM	-1.0	-1.1	-1.0	-0.5
Hitam	Adult	Female	PTM	0.3	-0.9	0.8	-0.6
Jagindas	Adult	Male	PTM	0.7	0.4	3.2	1.7
Kurus	Adult	Male	PTM	0.0	1.0	0.3	0.1
Manis	Adult	Female	LTM	-1.0	1.3	-0.6	-0.9
Panjang	Juvenile	Male	LTM	0.5	-0.5	-0.5	1.6
Penat	Adult	Female	PTM	1.3	0.6	0.4	-0.6
Pirate	Adult	Male	LTM	-1.0	-1.0	-0.1	-0.4
Tabu	Juvenile	Male	Hybrid	-0.7	-0.8	-0.2	-0.3
Trouble	Juvenile	Female	PTM	0.3	-1.0	-0.3	1.6
Mean EPG				220.34	3021.07	337.81	30.55
Standard Deviation				153.32	2603.05	335.60	33.91
Median EPG				224.20	3410.03	264.85	13.75
Min. EPG				58.77	258.9	0	0
Max. EPG				478.41	8687.08	1911.11	87.57
*Numbers reflect cysts per gram of faeces (CPG)							

Mean EPG counts were not normally distributed across age, sex, or species categories (Appendices 6.2-6.4). There were no statistically significant differences in PSR or EPG values between sex classes (Table 6.2). However, a juvenile female pig-tailed macaque was a statistical outlier in a sex-based analysis of *Strongyloides* sp. EPG (Appendix 6.5).

TABLE 6.2. Results of a Mann-Whitney U test for differences between mean PSR and EPG based on categorical variables.

Parasite	Sex*			Age**		
	Mann-Whitney U	<i>z</i>	<i>p</i>	Mann-Whitney U	<i>z</i>	<i>p</i>
<i>Trichuris</i>	20.0	-0.143	0.945	14.0	-0.169	0.937
<i>Balantidium</i>	26.0	0.714	0.534	5.0	-1.690	0.112
Unk. <i>strongylid</i>	24.0	0.429	0.731	11.0	-0.676	0.573
<i>Strongyloides</i>	8.0	-1.860	0.073	25.0	1.693	0.112
Richness	15.5	-0.792	0.445	24.5	1.619	0.112

* males (*n*=6) and females (*n*=9).
** adults (*n*=12) and juveniles (*n*=3)

There was also no statistically significant difference between mean PSR or mean EPG for any of the parasites with respect to age category (Table 6.2). However, the small sample size of juveniles (*n*=3) compared to adults (*n*=9) may render any meaningful interpretation of these data difficult. There were no significant differences between species categories regarding mean PSR ($F=1.564$, $p=0.457$), *Trichuris* sp. ($F=2.744$, $p=0.254$), *Balantidium* sp. ($F=1.011$, $p=0.603$), or *Strongyloides* sp. ($F=0.933$, $p=0.627$) values. However, there was a significant difference in the unknown strongylid EPG between species ($F=6.154$, $p=0.046$). A one-way ANOVA supported these results, and a Games-Howell *post-hoc* analysis revealed that there was an increase from a median value of 110.5 EPG in long-tailed macaques to 449.2 in pig-tailed macaques (95% CI, 71.5-

518.2, $p=0.013$). Mean PSR values in hybrids appear to be closer to those of the pig-tailed macaques compared to the long-tailed macaques, but a larger sample size with a more even age distribution would be necessary to make any definitive conclusions (Figure 6.2).

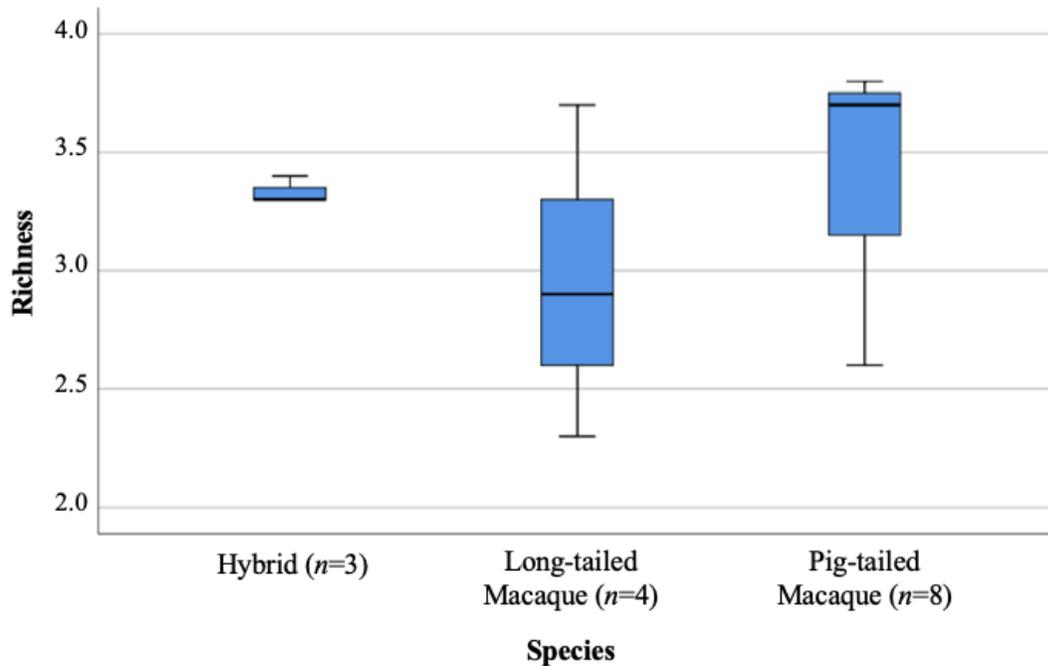


FIGURE 6.2. Box plot demonstrating the mean PSR for each species over the 10-month study period. Differences between the groups were not significant ($F=1.564$, $p=0.457$).

6.4.2 Strata Use

There was a slight but significant difference in the proportion of time spent on the ground between age categories (Odds ratio = -0.03143 ; Std. Error: 0.1591 ; z-value = -1.975 , p-value = 0.048 ; Residual deviance = 564.1 - on 1867 degrees of freedom; Null deviance = 586.22 on 1870 degrees of freedom). Adults spent approximately 25% of their time on the ground compared to 19% in juveniles. This effect held when controlling for species categories. Long-tailed macaques were significantly less likely to spend time on the

ground compared to the pig-tailed macaques across both age categories (Odds ratio = 0.3965; Std. Error: 0.1650; z-value = -2.403, p-value = 0.0163; Residual deviance = 564.1- on 1867 degrees of freedom; Null deviance = 586.22 on 1870 degrees of freedom). There was no significant difference between the hybrids and either the long-tailed macaques or the pig-tailed macaques.

6.5. Discussion

6.5.1 Comparisons with Prior Research

Research on parasite prevalence in long-tailed macaques and proboscis monkeys along the Lower Kinabatangan Wildlife Sanctuary (LKWS) in Sabah yielded the same four genera as the current study, and a host of others, including *Fasciola* sp., *Taenia* sp., *Anatrichosoma* sp., and *Ascaris* sp. (Frias et al., 2018a; Frias et al., 2019; Klaus et al., 2018; Salgado-Lynn, 2010). In total, approximately 14 unique genera were reported for the long-tailed macaques' faeces. Salgado-Lynn (2010) reported EPG values of approximately 79 and 300 for *Trichuris* sp. and strongylid sp. from long-tailed macaques, respectively. The reported value for *Trichuris* sp. is lower than the mean found at Sepilok (220.34), however it is well within the range of infection (58.77-478.41). The mean EPG value for the unknown strongylid sp. was only 333.09, barely lower than the current reported value of 337.81 at Sepilok. Despite a distance of only 60 km or so, macaques within the LKWS inhabit a considerably different environment compared to Sepilok. Regular fluctuations in the height of the Kinabatangan river combined with precipitation mean that the microclimate on the ground within the riverine corridor differs from the primary dipterocarp forest found within the Sepilok-Kabili Forest Reserve, which could facilitate the survival of soil-dwelling parasites (Eckhart et al., 2006; Harun, Dambul,

Abdullah, & Mohamed, 2014). Although no published data exist at present, an examination of the parasites found within the soil at both sites might help illustrate the effects of environmental variables on parasite dynamics within eastern Sabah.

Wenz-Mücke et al. (2013) reported drastically different mean EPG values for wild long-tailed macaques in northeastern Thailand, regardless of the level of contact with humans. *Trichuris* sp. and *S. fuelleborni* were reported as having mean EPG values of 30.4 (range: 9.5-44) and 212 (range: 0-673), respectively. EPG values for both categories were positively correlated with time spent on the ground and the likelihood of accepting human food (Wenz-Mücke et al., 2013). Given that the nutritional content and cleanliness of this gifted or stolen food is likely to vary, it is difficult to know whether the improved access to nutrition outweighs the risk of consuming contaminated food.

6.5.2 Parasite Species Richness

There are several non-mutually exclusive reasons that might account for low PSR values in the Sepilok group. Unique genera with low prevalence rates may have been missed during microscopic examination. However, any potential features were photographed and shown to several parasitologists to confirm their (lack of) significance. Parasites that occurred at a similar frequency to the ones identified above were unlikely to have been missed entirely. Relatively low species richness could also be the result of a sampling bias given that an average of only ~1.5 samples per monkey, per month were collected.

Low PSR could also be a consequence of the unique ecological niche in which the macaques live. Inter-specific variation in PSR often reflects differences in behaviour and/or habitat characteristics (Poulin, 2014). The genus *Macaca* illustrates this pattern well given that long-tailed macaques are more likely to inhabit heavily altered landscapes

compared to pig-tailed macaques (Hamada et al., 2011; Kurland, 1973; Moyes et al., 2016). The Kabili-Sepilok Forest Reserve is no exception considering that groups of long-tailed macaques appear to be absent within the lowland dipterocarp forest. Strata analysis at Sepilok revealed that pig-tailed macaques were more likely to be found on the ground compared to long-tailed macaques, which suggests that species-specific behavioural patterns hold true even in a hybrid group. Differences in body-size and habitat preference, however, may be negligible when the two species are overlapping so much that they are able to form a hybrid group (Fooden, 2006; Malaivijitnond et al., 2012). The nearby Kinabatangan river may provide another potential location to explore hybridization and parasite prevalence because long-tailed and pig-tailed macaques are often seen at the same location, occasionally even within the same tree. Pig-tailed macaques, however, are largely limited to the smaller tributaries whilst long-tailed macaques range near tributaries and the river itself (L. Gilhooly, personal observation).

These potential differences in habitat preferences make the group behaviour of the hybrid group all the more difficult to quantify. While interesting from a phylogenetic perspective, the unique group composition complicates any comparisons between this study and others that focused on parasite prevalence or species richness in macaques.

6.5.2 Stress and Parasite Ecology

Stress caused by tourists and associated infrastructure (e.g. vehicles) is an often-cited example of tourism's negative impact on wildlife health. It is tempting to assume that tourism is inherently stressful, and thus predisposes wild primates to experience compromised immune systems and inflated rates of morbidity and mortality (see Sponsel, 1997:11). There is indeed reason to believe that tourism can activate the stress response

in primates (Ruesto, Sheeran, Matheson, Li, & Wagner, 2009) and that both prolonged physiological stress and being immunocompromised might increase an individuals' susceptibility to infectious disease (Jones-Engel, Engel, Schillaci, Babo, & Froehlich, 2001; Kaur & Singh, 2009; Woodford, Butynski, & Karesh, 2002). However, in order to make such a damning conclusion about tourism specifically, tourism must be shown to consistently cause an activation of the hypothalamic-pituitary-adrenal (HPA) axis, which would lead to subsequent fitness consequences (Woodford, Butynski, & Karesh, 2002). In reality, very few studies on primates have explored these behavioural and physiological effects in tandem (Beehner & Bergman, 2017). Furthermore, tourism practices (and associated impacts on wildlife) will differ depending on the geographic area, the species at hand, and the level of staff intervention present (see chapter 2, this volume). The macaques in this study did not exhibit any obvious ongoing signs of stress such as stereotypical (i.e. repetitive) behaviour or prolonged eye contact with tourists.

Tourism influences aside, an exploration of stress, immune function, and parasitology is further complicated by the fact that a high rank may predispose an individual to higher parasite prevalence rates (increasing their risk of infection) while also affording them greater access to higher quality foods and social partners, which can decrease their risk of morbidity and mortality (MacIntosh et al., 2012). Research on stress and primates' susceptibility to parasites will also need to account for correlations in aggression. Higher rates of aggressive behaviour will likely result in more close contact with conspecifics, which can facilitate the spread of ectoparasites or those that are spread via the faecal-oral route. The potential for a positive correlation between faecal cortisol and parasitism does not necessarily imply a causal relationship between the two (Zohdy, Bisanzio, Tecot, Wright, & Jernvall, 2017).

Rank may also muddy explorations of stressors and immune function because high ranking individuals may be more or less likely to encounter tourists depending on their behavioural patterns. For example, the highest-ranking macaque in this study group interacted with tourists less often than most conspecifics, but his interactions were almost always aggressive (see chapter 4, this volume), which may result in a disproportionate activation of the HPA axis. Therefore, any evaluation of the stress response on an individuals' immune function and associated risk of parasite infection will need to account for the species-, sex- and rank-specific patterns in hormone levels. In addition to the introduction of novel anthropozoonotic pathogens, it is worth considering how the activation of the stress response might exacerbate parasite infection, and how this might be further compounded by the negative effects of anthropogenic land conversion or increasingly erratic climatic patterns.

6.5.3 Intra-group Contamination

The location and frequency of use of sleeping sites could be an important contributing factor to the spread of parasites within a group of primates (Chapman et al., 2012; Chapter 5, this volume). Repeated use of the same sites could facilitate the spread of parasites within a group through contaminated tree branches or soil, especially considering the fact that many macaques will defecate upon waking in the morning (Albert, Savini, & Huynen, 2011). Sampling the soil at sleeping sites at increasing intervals since their last use could allow future researchers to assess the importance of this behavioural factor on within-group parasite transmission.

6.5.4 Extra-group Contamination

Different macaque species with varying niche occupation strategies often overlap throughout south and southeast Asia (Fooden, 2006; Moyes et al., 2016). Long-tailed macaques have been shown to be sympatric with pig-tailed, rhesus (*M. mulatta*), stump-tailed (*M. arctoides*), and Assamese macaques (*M. assamensis*) (Hamada et al., 2011; Linkie, Dinata, Nofrianto, & Leader-Williams, 2007). At Sepilok, however, there was no evidence of long-tailed macaque groups. One other group of pig-tailed macaques was observed at Sepilok, which included a single long-tailed macaque male. There was no evidence of hybrid individuals within that group. The lack of long-tailed macaque groups within the study area is consistent with research that found that long-tailed macaques prefer secondary, degraded, and anthropogenic habitats (Hamada et al., 2011). Thus, the risk of contamination from long-tailed macaques should have been considerably reduced.

Klaus et al. (2018) found that anthropogenically-managed proboscis monkeys at Labuk Bay, Sabah had significantly higher parasite prevalence and EPG levels compared to their wild counterparts along the Kinabatangan river. However, the Labuk Bay groups also experienced a density that was 10x greater than found in the wild. This inflated group density does not appear to be a concern at Sepilok considering there was only one other group in the area. The study groups' encounters with the single pig-tailed macaque group were rare and typically fleeting, although one of the juvenile hybrid males was seen playing with the long-tailed macaque male on one occasion. Therefore, inflated group density and subsequent risk of exposure to extra-group macaques' parasites should have been low (Chapman et al., 2012). On the other hand, the hybrid group encountered orang-utans almost daily and occasionally came within 20 m of gibbons and red langurs as well. The degree of overlap between the hybrid group and the home ranges of slow

lorises and tarsiers is not known, though both species inhabited the study area (S. Alsisto, pers. comm., 28 September 2016).

6.5.5 Diet

The macaques fed on provisions intended for the sun bears or orang-utans during 34% of the total observed feeding bouts (Chapter 5, this volume). This behaviour could contribute to parasite dynamics in a few potentially contradictory ways. Access to supplemental nutrition could act as a buffer against parasite infection by improving immune function and reducing the ingestion of potential insect reservoirs, or it could serve to increase parasite exposure through surfaces contaminated with orang-utan faecal material (Murray, Becker, Hall, & Hernandez, 2016).

All of the parasites observed in the study group are spread via direct contamination, though others are known to be carried by invertebrate hosts (Cormier & Jolly, 2017). Invertebrates constituted approximately 36% of feeding bouts witnessed across all age and sex categories during behavioural observation, which highlights the potential for invertebrates to act as a source of infection. Exposure to these parasites is less likely to be affected by macaque behaviour, such as grooming or coprophagy (MacIntosh, 2014).

Orang-utan provisions alone constituted 18% of the total observed feeding bouts. Although the food itself may not have been handled or bitten by orang-utans prior to consumption, these feeding bouts involved coming into contact with surfaces that are touched by the orang-utans daily, including the feeding platforms, ladders, ropes, and tree branches. The macaques were never observed biting, scratching, or climbing on the orang-utans, so the risk for the transmission of parasites that are spread through social

contact appears low. Having a better understanding of the parasite species richness (and modes of transmission) of the Sepilok orang-utans might help to elucidate the impact of parasite sharing via contaminated strata at Sepilok. Currently orang-utans are only screened for parasites by the veterinary staff at SORC after displaying signs of illness.

Despite this potential risk of exposure to novel parasites during these feeding bouts, there is a precedent for supplemented diets resulting in lower parasite burden in wild primate groups (Agostini et al., 2017). Weyher et al., (2009) found that a group of baboons who routinely raided garbage had lower helminth burden compared to a group that did not. These findings supported research that showed that crop raiding groups were typically in better condition and experienced greater reproductive success when compared to those who subsisted on wild food alone (Lane-deGraaf et al., 2010).

The current study groups' diet that is supplemented with fruit and vegetables (as opposed to human 'junk food', such as ice cream) could have a mitigating effect on the parasite richness and intensity of infection by reducing exposure to insect vectors and by buffering individuals against infection. Sepilok thus provides a opportunity to explore the effects of a supplemented diet on parasite dynamics. However, these data should ideally be coupled with results from macaque groups experiencing different levels of human provisioning. Such groups could include those that have access to a more diverse supply of human food (e.g. those who raid trash bins), those who do not supplement their diet with human food (e.g. within primary or secondary forest), and/or other groups that live within wildlife rehabilitation centers and have access to provisioned fruit and vegetables (e.g. Semenggoh Nature Reserve in Sarawak). Such findings could help illustrate the relative importance of diet on the immune function and parasitology of wild macaques.

6.5.6 Locomotion

Parasite avoidance strategies, including locomotion behaviour, may be motivated by the disgust response and are likely to differ between species categories (Curtis, 2014; Nunn, Gittleman, & Antonovics, 2000). While exposure to contaminated soil, food, or water is a necessary evil in an attempt to find nutrients, unnecessary exposure to such contaminants during locomotion could be costly in terms of an increased risk of infection (Curtis, 2014; Curtis, Aunger, & Rabie, 2004). If parasite avoidance is a strategy that individuals learn over time, infants and juveniles may be less likely to avoid potentially high-risk strata such as mud and water.

Juvenile macaques across all species categories had a higher mean *Strongyloides* EPG count compared to the adults, though the difference was not significant. These results are preliminary based on the small sample size, but the trend towards a higher EPG in juveniles complements findings where juvenile Japanese macaques experienced significantly higher prevalence and EPG of *T. trichiura* and *S. fuelleborni* compared to adults (MacIntosh, Hernandez, & Huffman, 2010). The fact that many helminth species are encountered in soil suggests that locomotion patterns and exposure to contaminated strata could play a role in overall risk of infection (Wenz-Mücke et al., 2013). However, analysis of strata use suggested that juvenile individuals actually spent less time on the ground compared to adults. This is contrary to findings on disgust and parasite avoidance in humans, where the behavioural tendency to avoid stimuli associated with infection decreases slightly with age (Curtis, Aunger, & Rabie, 2004). Although the locomotion data from this study did not support this hypothesis, collecting behavioural data from more fine-grained age categories within a single species may yield more conclusive results.

Terrestrial locomotion was believed to be a contributing factor to the high parasite prevalence seen in ring-tailed lemurs (*Lemur catta*) compared to the more arboreal Verreaux's sifaka (*Propithecus verreauxi*) (Loudon & Sauther, 2013). Fluctuations in rainfall and, thus, exposure to water in the environment, have been targeted as contributing factors to parasite prevalence in primate species (Lane et al., 2011). Pig-tailed macaques in the hybrid group were more likely to be observed on the ground compared to long-tailed macaques, which both reflects species-specific trends in locomotion and may indicate an increased risk of exposure to soil-dwelling parasites.

6.5.7 Limitations

There are myriad biological and social processes that may affect both the exposure to parasites and the risks of morbidity and mortality, many of which are not independent from each other and are poorly understood (Poulin, 2014). As such, a comprehensive exploration of the causes and effects of parasite infection in the current study group is beyond the scope of this paper. Although it is hoped that the results of this preliminary examination of parasites in a hybrid macaque group will be useful for future researchers, there are several limitations to this study that need to be addressed. These limitations include general challenges that are true for all parasite research, as well as problems that plagued this project specifically.

Although over 200 faecal samples were recovered from known individuals, collecting the required 3-4 per individual per month that is recommended by Poirotte et al. (2016) to make a conclusion about individual and group prevalence was not possible. Faecal sample collection was hindered by a longer-than-average rainy season as well as the study groups' propensity to sleep in large dipterocarps that exceeded 25 m, which largely prevented the observation of defecation. The timing of the macaques' descent from their sleeping site also appears to have had an impact on faecal collection rates. When the macaques slept near boardwalks they would often descend soon after waking (~0630h) and rest on the railings for upwards of an hour before moving on. These locations made faecal sample collection easier because multiple macaques could be observed at once, especially as they moved to defecate (Figure 6.3).



FIGURE 6.3. The group rests on the railing at BSBCC in the early morning after descending from their sleeping site. Picture by L. Gilhooly.

6.6. Conclusions

6.6.1 Current Findings

This study highlights the complex nature of investigating parasite prevalence and richness in a unique primate group. While overall PSR was low within the hybrid macaque group at Sepilok, there was a

considerable range in EPG values across individuals. Pig-tailed macaques appeared to harbor more eggs from the unknown strongylid group when compared to long-tailed macaques and they also spent more time on the ground. Differences in prevalence and behaviour were not significant when the hybrid individuals were compared with either long-tailed or pig-tailed macaques. Neither age nor sex appeared to influence EPG or richness values within the group.

6.6.2 Next Steps at Sepilok

Future research at Sepilok should focus on the PSR of the orang-utans, sun bears, other endemic primate species, as well as the local staff and other researchers in order to quantify the degree of existing overlap. Collecting parasite data from other naturally-occurring hybrid groups (e.g. those that are comprised of endemic macaque species) would be an interesting comparison to data from Sepilok given that parasite genera are likely to vary geographically.

Predicting the likelihood and extent of parasite transmission between humans and non-human primates in anthropogenic environments will require genus or, ideally, species-level identification from both communities. Species that can readily infect humans and other non-human primates represent the greatest risk for crossover events, which means that primates may act as a reservoir for parasites that can cause illness in humans and vice versa. *Trichuris* sp., which was the second most common parasite found in this study, is a good example of this phenomenon because *Trichuris* sp. are capable of infecting multiple primate species, which makes them a reservoir for human whipworm in areas where the species and strain are identical (Yao, Walkush, Shim, Cruz, & Ketzis, 2018). Understanding the transmission pathway of these shared parasites is also

important for predicting the risk of parasite transmission. Socially transmitted parasites may be more of a threat in areas where primates interact with humans frequently, either as photo props for tourists or as food source for local residents. Parasites that are spread through the environment (e.g. soil-transmitted helminths) may be more of a threat to primates who experience significant overlap with human settlements, such as in cities like Jaipur or Singapore (Loudon & Sauther, 2013; Moyes et al., 2016).

However, species- or population-level risk of infection is only part of the story. An ecological approach to parasitology allows researchers to consider the differential impact of parasitism depending on the individual. Rank, diet, and species-specific behaviour (e.g. group fission patterns) may mitigate high rates of exposure to helminths in the environment or via direct transmission (Balasubramaniam et al., 2019; Loudon & Sauther, 2013; MacIntosh, 2014; Poulin, 2007). The proximity of the current study group to tourist infrastructure, the effects of provisioning on ranging behaviour, and the potential for contamination from rehabilitating animals could challenge the hypothesis that a smaller home range size is associated with decreased exposure to environmental helminths (Freeland, 1976). Combining ecology-based data from non-human primates along with epidemiological and ethnographic data from human populations will allow researchers to identify communities that are most at-risk for infection with zoonotic or anthrozoonotic parasites (Cooper & Nunn, 2013).

6.6.3 Considerations for Future Primate Parasite Research

Collecting and processing fresh faeces for sedimentation or flotation microscopy techniques is fairly straightforward and inexpensive, but researchers should consider whether sufficient identification and documentation will be possible in the field

considering the wide array of potential helminth genera. In the event that a trained parasitologist is not at hand to make identifications, multiple high-quality images at different resolutions with an accurate scale for each parasite can help future identification. However, this is complicated by the fact that high-quality microscope cameras may not be accessible to small-scale projects. Reliance on *in-situ* identification alone may result in an underestimation of both genera and species prevalence. Researchers should endeavor to use molecular methods to confirm parasite identification whenever possible, while keeping in mind that the presence of unidentified or cryptic species will complicate the task (Cavallero et al., 2015; Frias et al., 2018b). These methods are becoming increasingly cheaper and more accessible. Accurate identification will help estimate the risk of cross-species infection while also allowing future researchers to track which parasites have been found in primate species throughout their range.

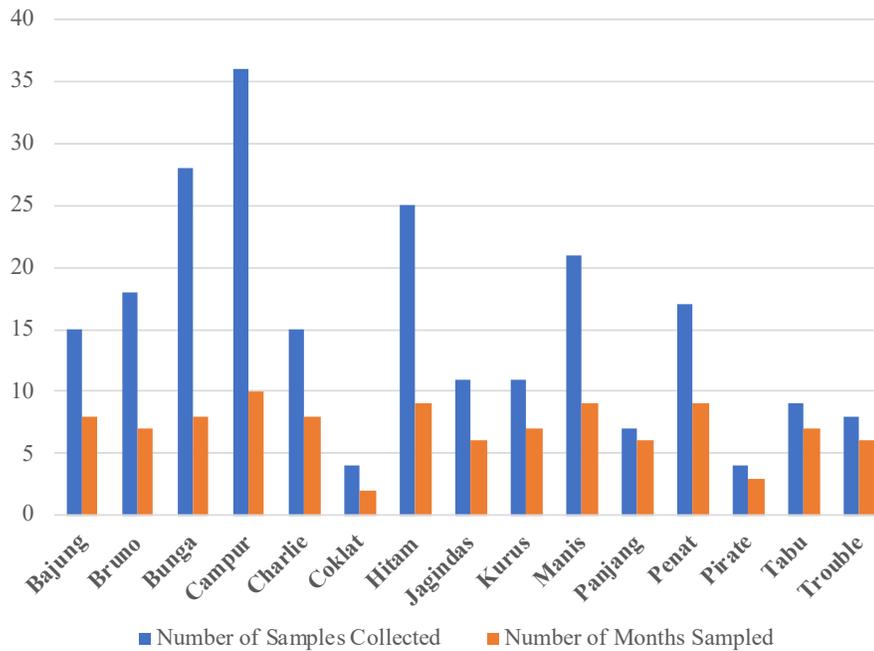
With the increased availability and popularity of molecular methods for parasite identification, future researchers may be tempted to incorporate parasitological data analysis into projects for which parasites are not the main focus. Parasites should not be included as opportunistic or supplemental data considering the amount of effort and resources that are required to do parasite research well. The location of a research project will also determine which reagents are available and accessible within a reasonable time frame. Some staining reagents may take upwards of six months to arrive, with others unavailable entirely due to flight restrictions. Cable et al. (2017) highlight the importance of the cumulative effects of biotic and abiotic influences on parasite ecology, which calls into question the function of parasite data that is devoid of its ecological context. Collecting robust accompanying data on group behaviour and diet, climate patterns,

habitat characteristics, and interactions with other relevant species are all time-consuming and require a significant amount of background research and expertise. These data should not be collected as an afterthought; an absence of this accompanying information will make meaningful interpretation of parasite richness and prevalence difficult. Consulting with parasite experts and developing a plan for data collection and analysis prior to fieldwork should improve the utility of parasite data while avoiding the pitfalls of inadequate data collection.

Ideally, faecal samples should be collected from known individuals 3-4 times within a span of 10 days to get an accurate snapshot of a focal animal's parasite richness (Poirotte et al., 2016). This may be difficult to do depending on the movement patterns of the study group, individual patterns of defecation, the expertise of the research staff, as well as the researchers' ability to move freely within the groups' home range. Allocating specific days or times of day for faecal collection may improve one's collection rate, but this may require sacrificing other kinds of data (e.g. behavioural data, group movement data, etc.).

The combination of biotic and abiotic factors that affect parasite acquisition means that a multidisciplinary approach that includes social, environmental, and biological factors may better address the growing concern of infectious disease emergence at the human-wildlife interface (Balasubramaniam et al., 2019). Carefully designed studies that measure the effects of anthropogenic influence on the morbidity and mortality of wild primates will allow us to identify location- and species-specific interventions to reduce the likelihood of disease transmission.

6.7 Appendices



APPENDIX 6.1. Summary of each macaque that was sampled during the study period.

	Age	Shapiro-Wilk		
		Statistic	df	Sig.
Richness	Adult	0.942	10	0.571
	Juvenile	0.923	3	0.463
<i>Trichuris</i>	Adult	0.891	10	0.176
	Juvenile	0.893	3	0.364
<i>Balantidium</i>	Adult	0.954	10	0.713
	Juvenile	0.937	3	0.516
Strongylid	Adult	0.936	10	0.512
	Juvenile	0.841	3	0.216
<i>Strongyloides</i>	Adult	0.731	10	0.002*
	Juvenile	0.772	3	0.048

* Statistically significant at $p \leq 0.05$.

APPENDIX 6.2. Tests of normality for PSR and mean EPG divided by age categories.

	Sex	Shapiro-Wilk		
		Statistic	df	Sig.
Richness	Male	0.889	6	0.312
	Female	0.916	7	0.440
<i>Trichuris</i>	Male	0.972	6	0.905
	Female	0.9	7	0.331
<i>Balantidium</i>	Male	0.946	6	0.705
	Female	0.948	7	0.714
Strongylid	Male	0.878	6	0.260
	Female	0.961	7	0.823
<i>Strongyloides</i>	Male	0.859	6	0.186
	Female	0.612	7	0.000*

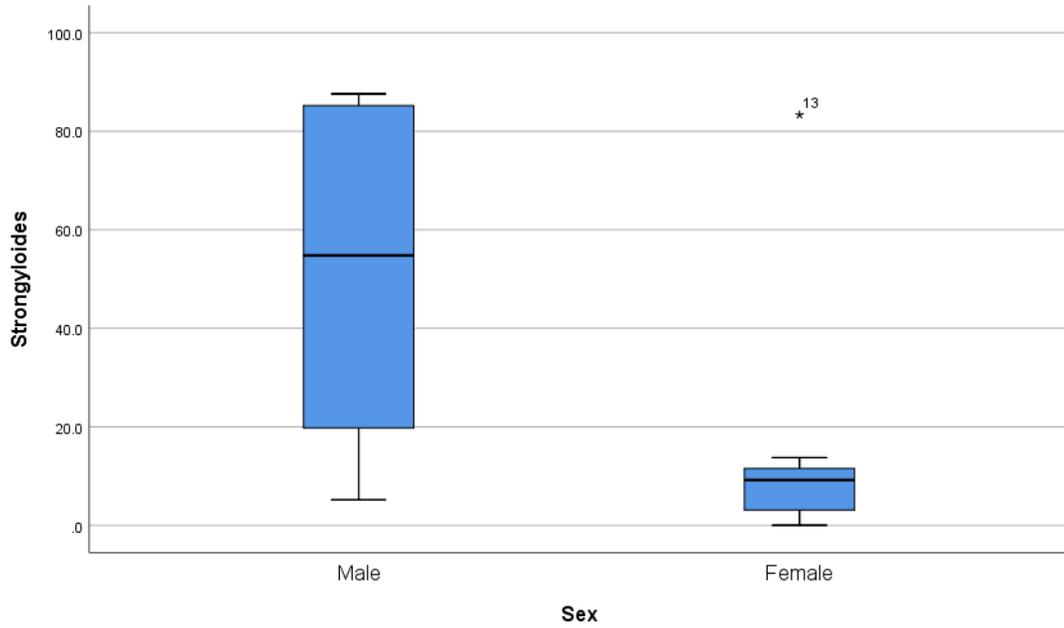
* Statistically significant at $p \leq 0.05$.

APPENDIX 6.3. Tests of normality for PSR and mean EPG divided by sex categories.

	Species	Shapiro-Wilk		
		Statistic	df	Sig.
Richness	Hybrid	0.75	3	0.000*
	LTM	0.993	3	0.843
	PTM	0.837	7	0.093
<i>Trichuris</i>	Hybrid	0.833	3	0.195
	LTM	0.797	3	0.106
	PTM	0.965	7	0.858
<i>Balantidium</i>	Hybrid	0.98	3	0.730
	LTM	0.99	3	0.811
	PTM	0.877	7	0.214
Strongylid	Hybrid	0.945	3	0.546
	LTM	0.998	3	0.921
	PTM	0.947	7	0.706
<i>Strongyloides</i>	Hybrid	0.996	3	0.878
	LTM	0.796	3	0.104
	PTM	0.833	7	0.085

* Statistically significant at $p \leq 0.05$.

APPENDIX 6.4. Tests of normality for PSR and mean EPG divided by species.



APPENDIX 6.5. Box plot detailing the EPG values of *Strongyloides* sp. in male (n=7) and female (n=8) macaques across age and species categories. Note that the results were likely not statistically significant due to the disproportionately high EPG values from one female macaque.

6.8 References

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7 Conclusion

7.1 Summary

The strength of ethnoprimateology lies in its ability to incorporate several methodological approaches in order to explore topics that are fundamentally multi-species, multi-ethnic, multi-disciplinary, and rooted in historical and contemporary economic relationships (Riley, Fuentes, & Dore, 2017). This project has relied on an ethnoprimateological approach to understand why some tourists seek out experiences with wildlife, how their presence affects the behaviour and ecology of wild macaques, and how to better predict and prevent the undesirable outcomes of nature-based tourism.

In chapters 3 and 4 of this dissertation, results from the semi-structured interviews, participant observation of the tourists, and behavioural data collection on the macaques makes it clear that we need to identify specific problematic tourist behaviour in order to prevent it. Most simply, this involves identifying tourist behaviour that is likely to cause an aggressive reaction from the wild primates and designing educational material that addresses such risky behaviours. Moreover, understanding the motivations and perceptions of tourists who are visiting a rehabilitation site, such as Sepilok, will help identify common gaps in visitors' knowledge about important safety concerns, including the risks of infectious disease.

In chapter 5, I describe the impact of consistent access to provisioned food on the sleeping and foraging patterns of the wild macaques at Sepilok. These results suggest that generalist species can benefit from proximity to rehabilitation centers, particularly when

the provisioned food is of a high quality and not associated with conflict with visitors. Furthermore, the macaques do not appear to drastically avoid the tourist area, which suggests that they do not attempt to avoid close proximity with visitors. Access to such supplemental nutrition could hypothetically affect the prevalence and intensity of parasite infection in wild macaques, as I describe in chapter 6 in an effort to highlight some of the potential next steps in assessing parasite ecology at Sepilok.

A critical analysis of primate tourism at any location requires consideration of species-specific behaviour coupled with an understanding of the issues surrounding tourism, particularly in terms of the impact on the local environment (Fletcher, 2019). The perceptions and experiences of tourists are likely to shape individual encounters between visitors and wild animals (Soulsbury & White, 2015), which makes a one-size-fits-all approach to educational programs woefully inadequate. The goals of animal caregivers, community hosts, and tourists are affected by myriad cultural and political forces, and it is unreasonable to expect that they can reach a consensus on what the best course of action is when it comes rehabilitation centers like Sepilok (Chambers, 2010)

As a kind of liminal site that attracts a wide variety of tourists, Sepilok highlights how difficult it can be to satisfy the desires of tourists while protecting the well-being of both rehabilitating and wild primates. This research highlights many of the systematic challenges associated with wildlife tourism; on an individual scale, visitor behaviour may affect primates and subsequent rates of aggression, while the cumulative effects of proximity to anthropogenic spaces may alter primate behaviour and the concomitant exposure to potentially lethal pathogens (Wallis & Lee, 1999).

All nature-based tourist sites should evaluate the costs and benefits of inconveniencing visitors for the sake of animal welfare (Goldsmith, 2014). It is crucial to

mitigate the risks of infectious diseases and psychological stress while acknowledging that not all animals are affected equally. Routine provisioning of nutrient-rich food, such as the kind seen at Sepilok, may benefit generalist species like macaques so long as steps are taken to ensure their safety and well-being. Based on the findings of this study, I suggest that: i) all tourist sites limit visitors' access to food, either by using a locker system like the one at Sepilok and/or by stopping the sale of food on site; ii) places that feature macaques should post multilingual warning signs about the dangers of making eye contact with primates; and iii) staff should wear personal protective equipment in order to limit the risk of contamination of provisions while also signaling to visitors that infectious disease is risk that should be considered. Evidence-based studies that identify risks and outcomes that are specific to primate species or particular types of sites (such as wildlife rehabilitation centers) will allow site directors and staff to make their own decisions about relevant visitor policies and educational materials.

7.2 *Next Steps*

This study provided preliminary information on how to reduce the negative effects of tourism on wild macaques at wildlife rehabilitation centers. It would be helpful to gain a better understanding of how this supplemental nutrition affects immune function, fecundity, and infant survival. More in-depth knowledge of the health of the macaques may help to inform Sepilok staff about the risk of infectious diseases being passed directly to the orang-utans (and to a lesser extent, the sun bears). This is important because of both the precarious conservation status of the orang-utans and sun bears, as well the potential effect on their successful rehabilitation.

Wildlife tourism and conservation is inherently multi-disciplinary. No single approach can capture the complexity of economic and cultural interests colliding with infectious disease, ecology, and conservation biology (Soulsbury & White, 2015). As long as funding agencies sort disciplines into discrete categories, researchers involved in tourism will be forced to narrow their focus in order to write competitive proposals. Anthropologists should continue to examine wildlife tourism and disease with an ethnoprimate lens, while striving to develop collaborative projects with parasitologists, geneticists, and epidemiologists to ensure that research on the etiology of infectious disease is thorough and replicable (Balasubramaniam, Sueur, Huffman, MacIntosh & 2019). At Sepilok, this may involve examining the parasite ecology of the macaques, orang-utans, and sun bears to see whether or not there is evidence of transmission between species. More research on the efficacy of education programs will also allow for better tourist management at Sepilok and beyond. A collaborative, multi-disciplinary approach will better tackle the intersection of culture and biology that occurs at the human-wildlife interface of nature-based tourism.

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