Understanding drivers of parasite infections in baboons: insights across multiple levels, from populations to genetics

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By

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Photo of chacma baboons at the Tsaobis baboon project. Cassandra L. Raby

ABSTRACT

Parasites play an important role in evolutionary processes and regulating host populations. Furthermore, parasites have the ability to result in economically and physically disruptive diseases which are becoming increasingly common as anthropogenic change disrupts the ecology of host-parasite systems. Exploring the drivers that influence parasite transmission and infection can further our understanding of host-parasite relationships and how these might change in the future. Such drivers occur across multiple scales, with different factors influencing host exposure and susceptibility to infection across species, across populations, and across individuals and groups within populations. In this thesis, I investigate these drivers across multiple scales. I begin by analysing the patterns of gastrointestinal parasite communities across species of the genus *Papio* (baboons), and then focus my observations on a population of wild chacma baboons (*Papio ursinus*) in Namibia. I focus on primates due to their zoonotic potential and the fragility of some primate populations to extinction; I focus on baboons because in Africa it is this primate taxon that may be of greatest significance for human health: their wide distribution and coexistence with people living in rural and urban populations make them a likely source of zoonotic pathogen transmission. To explore the drivers of gastrointestinal parasite communities and richness across *Papio* species, I conducted a meta-analysis assessing the importance of species differences and environmental conditions. I found that the parasite communities were widely shared across baboon species in Africa, and that the environment was more important than the host species in determining where specific parasite species occurred. I then went on to explore patterns of gastrointestinal parasite transmission and infection across individuals in the chacma baboon population in Namibia. First, I explored how spatial heterogeneity in the environment shapes the risk of parasite transmission and whether the baboons practice avoidance behaviours at the troop level. I identified those habitats that might be better suited for parasite cyst and egg survival, and found that the baboon troops avoided revisiting these areas when they had already been exposed to parasite infection. In the next two chapters, I assessed whether two components of individual variation, sociality and genetic diversity, shaped exposure and susceptibility to parasites. In the first, I found no evidence that social network position influenced parasite infection. However, in the second, I found that inbreeding and *Mhc-DRB* allelic richness were associated with infection by some parasite species. Overall, the findings of my thesis highlight the myriad ways in which the environment, host behaviour, and host heterozygosity can influence host-parasite interactions – at the multiple scales of the individual, social group, population, and species.

ACKNOWLEDGMENTS

The first discussions about this PhD project started in 2011 after my first field season with the Tsaobis baboon project, and between then and now there have been a lot of time to fill with (mis)adventures. With that in mind, there are so many people to thank, so many friends I have made, and this section will never be able to do justice to the amount of support I've received throughout.

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As I switch between cities and departments, it would have been easy to get lost and to feel isolated. However, I never felt that for a moment thanks to all my wonderful friends at the Institute of Zoology, where the Wellcome building really lives up to its name (see what I did there?). And to the Institute of Integrative Biology, where I made so many wonderful friends. To everyone who I've worked alongside in any way, and at any stage of this PhD, you've helped make this journey so much better.

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CHAPTER ONE

Introduction

OVERVIEW

The overall aim of this thesis is to explore the individual-, population-, and species-level determinants of parasitic infections in wild baboons, with the intention to better inform predictions of the risk of zoonotic disease outbreaks as a result of anthropogenic change. Zoonotic diseases are particularly important, given that they are now the most common source of emerging infectious diseases (EIDs) in human populations (Jones et al., 2008). I focus on wild primates, rather than other wild taxa, for two reasons. First, primates are a major source of EIDs (e.g. HIV: Keele et al. 2006), reflecting their close evolutionary relationship to ourselves. Second, the majority of primate species are threatened with extinction, and thus also at risk from disease outbreaks (Chapman et al., 2005). Both points make an understanding of the links between anthropogenic change and disease risk in this group especially important. This introductory chapter aims to provide a broad context to the general issues explored in this thesis, and to provide an outline of the thesis structure.

THE IMPORTANCE OF PARASITES

Parasitism, when considered broadly to refer to any species with obligate feeding on a host without resulting in its death, is considered one of the most successful lifestyles of all organisms (Poulin, 2011). Most, if not all, free-living species are associated with at least one parasite species, and because of this, it has been claimed that the majority of species are parasites, making them the biggest component of diversity on the planet (Windsor, 1998). More conservative estimates still place parasites at making up 40% of life (Rohde, 1982), so parasites are clearly a common component of animal populations. Given their ubiquity, and the potential detrimental impact parasites can have on individual hosts (Tompkins & Begon, 1999), host population dynamics (Albon et al., 2002; Hudson et al., 1998) and ecological communities and ecosystems (Collinge & Ray, 2006; Holdo et al., 2009), there is a pressing need to understand the drivers of parasite infection, particularly in response to anthropogenic change. The work presented in this thesis aims to do that by examining the drivers of infection levels in a wild mammalian system, at the individual, population and species scales (Fig 1.1).

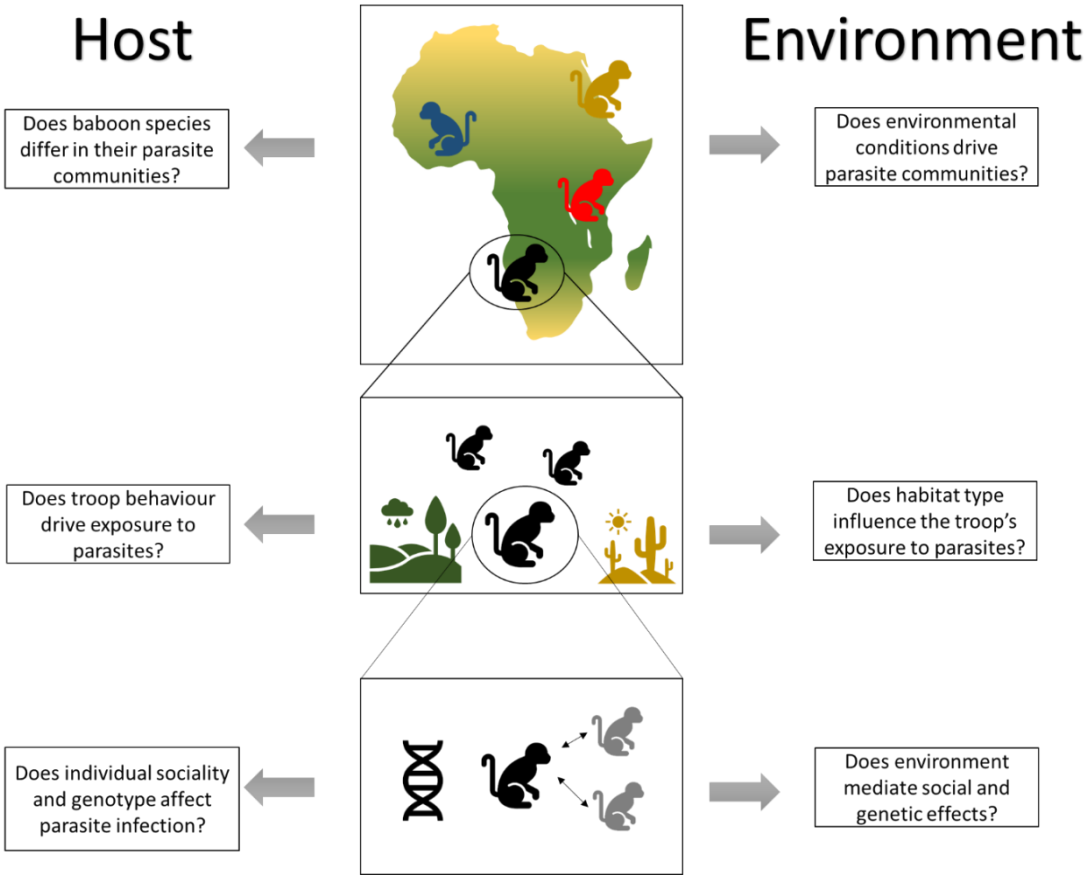


Figure 1.1. Overview of the research framework adopted in this thesis. My research questions cut across species, populations, and individuals (from top to bottom in this figure), and addresses the role of both the host and the environment in parasite infections.

PARASITES WITHIN INDIVIDUALS AND POPULATIONS

Parasite infection is invariably overdispersed among individuals within a population (Poulin, 2007). That is, parasite distribution within a host population is heterogeneous, with the minority of hosts infected by the majority of parasites (Shaw & Dobson, 1995). These distributions occur through two mechanisms: individual variation in their exposure to parasites, and individual variation in their susceptibility to infection (Anderson & Gordon, 1982a; Wilson et al., 2002). The likelihood of a host becoming infected is dependent on two processes. First, the host's encounter rate with parasite infective stages: infected hosts for close-contact transmitted parasites, free-living infective stages for environmentally-transmitted parasites, and vectors (intermediate host species) for indirectly-transmitted parasites. Second, the parasite's ability to successfully exploit their host. Both these stages are dependent not just on characteristics of both the host and parasite (e.g., genotype, behaviour etc.), but also on environmental conditions (McCallum et al., 2017). For this

reason parasite transmission dynamics, and host infection risk, are sensitive to anthropogenic environmental changes (Budria & Candolin, 2014). One specific concern about changes in the ecology of host-pathogen interactions is that these changes may give rise to emerging infectious diseases (EIDs), risking the health of humans and wildlife (Daszak et al., 2000).

PARASITES ACROSS POPULATIONS AND SPECIES

The most pervasive biogeographic factors that determine the spatial distribution of free-living species is latitude and the environmental gradients associated with it (Hawkins et al., 2003; Nekola & White, 2007; Poulin, 2003; Rohde, 1992). However, the determinants of parasite distributions may differ from those of free-living species. Instead of abiotic factors being the most important, biotic factors play an additional role as interactions between parasites and their host(s) and/or intermediate host(s) are key to their survival (Peterson, 2008). That said, those parasites with an external, free-living stage (e.g., cyst, spore, egg or infective larval stage) are prone to environmental influences on their survival, restricting their range to be within their ecological niche. When parasites occur within their host, be it their definitive host or an intermediate host, they are protected from the direct effect of environmental factors, particularly within vertebrate/mammalian hosts which are able to maintain a relatively stable internal environment. In these cases, the parasite's occurrence and fitness will be shaped by the conditions within the host and the host's response to the external environment (Gallana et al., 2013). Hence, patterns of parasite diversity are likely to be shaped by the characteristics of the host and parasite, and both must be considered in order to understand their ecology and distribution. Furthermore, anthropogenic change that alters the biotic and abiotic conditions of the environment, could have profound effects on the interaction between hosts and their parasites. Understanding these environmental drivers is therefore crucial if we are to understand how the distribution and abundance of parasites is likely to change in the future.

A valuable example of such environmental dependencies, and the impacts of anthropogenic change, can be seen among primates. Many primates live in habitats that are disrupted through human activities, including land conversion into agriculture and settlements, which results in fragmented habitats and altered food availability (Chapman & Peres, 2001). Furthermore, human activity is changing the climate globally and it is expected that this too will impact infectious disease prevalence (World Health Organization, 2003). Understanding

the environmental conditions associated with the parasites of baboons may be able to assist us in predicting the impact of these anthropogenic changes on non-human primates and, potentially, human health.

THE BABOON STUDY SYSTEM

Species of the genus *Papio* are an ideal model system with which to explore the ecological determinants of parasite prevalence for a number of reasons: their behaviour, life-history, and ecology are well studied (e.g. Altmann & Altmann 1970); they inhabit a range of habitat types (Winder, 2014); and they are a potential source of zoonotic parasites (e.g. Muriuki et al. 1998). Chapter 2 of this thesis describes the work carried out on baboons and their parasites in more detail but, briefly, multiple studies have reported the gastrointestinal parasites of baboons across baboon species, and this previous research includes a study of the intrinsic and extrinsic factors shaping parasite species richness in the Tsaobis baboon population (Benavides et al. 2012), the same population which forms the focus of this study. This highlights the potential of *Papio* baboons as a whole, and the Tsaobis population in particular, for studying the determinants of parasite infection at the individual-, population-, and species-level.

THESIS STRUCTURE

This project considers the drivers of exposure and susceptibility of baboon hosts to their parasites at multiple scales of biological organisation (Figure 1.1): across species and populations; within populations; and within individuals. To achieve this, the thesis is split into two parts. In the first part, I explore the macro-scale factors shaping parasite communities across baboon species using previous studies across multiple baboon populations. Thus, *Chapter two* is a literature review of the current knowledge of baboon-parasite relationships; and *Chapter three* is a meta-analysis assessing the patterns of parasite communities across *Papio* species in relation to continental-wide environmental gradients. The second part is a higher resolution investigation of a single baboon population, the Tsaobis baboons, where I explore the potential pathways through which biotic and abiotic factors shape exposure and susceptibility to parasite infection. In *Chapter four* I introduce the study population and methodology used for the following data chapters. To explore the population-level behaviour and environmental variation shaping parasite transmission, *Chapter five* investigates troop movement behaviour in relation to the spatial heterogeneity of parasite distribution. The

final two data chapters then consider how two individual-level factors, specifically individual sociality (*Chapter six*) and inbreeding and immune genes (*Chapter seven*), contribute to the exposure and susceptibility of a host to infection. The final Discussion chapter (*Chapter eight*) then summarises and synthesises the findings, and considers the broader implications of this work.

CHAPTER TWO

Gastrointestinal parasites in baboons: a review of their prevalence and drivers

INTRODUCTION

Parasitism describes the interactions between living organisms where one, the parasite, is dependent on another, the host, and where this interaction comes at a cost to the host (Zelmer, 1998). Parasites have been shown to play a key role in host population dynamics (Anderson & May 1978a; Dobson & Hudson 1992; Watson 2013) and evolutionary processes (Hamilton et al. 1990; Hamilton & Zuk 1982). Yet research into these dynamics can be difficult to observe in natural environments. One approach is to study diseases in wild animal populations where detailed information is available on individual demography and behaviour (Scott & Dobson 1989). Long-term field studies of wild primates provide one such opportunity. These studies have been providing insights into primate ecology and behaviour for decades (e.g. Altmann & Altmann 1970; Hrdy 1977; Fossey 1983; Goodall 1986), and can potentially allow us to explore parasite ecology in host species that are well-established study systems in their own right. Through such long-term studies we can begin to assess the drivers behind variation in the parasite richness (number of parasite species) and abundance (parasite burden within a host) infecting individual primates, and the prevalence of parasites (proportion of individuals infected) across primate populations. A key benefit of these long-term studies is the information they provide about individual host variation; many of these animals may have been followed throughout their lives and their individual characteristics, and relationships with their environment, well documented. For example, individual factors previously associated with parasites in primates have included: age; sex; body condition; social rank; and reproductive state (Nunn & Altizer, 2006a). Ecological factors, such as rainfall and temperature, and differences in troop behaviour, have also been previously associated with parasites in primates (Nunn, 2006a). These long-term studies can therefore provide an invaluable opportunity for understanding parasite communities in heterogeneous populations structured into discrete social groups living in different environments.

The study of primate parasites is particularly important in the context of emerging infectious diseases (EIDs), which introduce new risks to global health and the economy. In humans, the largest source of EIDs occurs from the zoonotic transfer of pathogens, and 70% of these events are from wildlife populations (Daszak, 2000; Jones, 2008; Taylor et al., 2001). Of these wildlife populations, primates are of particular importance. Almost 70% of primate parasites are capable of infecting multiple host species (Pedersen et al. 2005), with secondary hosts being those that are most genetically similar and in close geographic proximity (Davies & Pedersen 2008). Given their phylogenetic similarity to humans and often close geographic

proximity, primates are important potential sources of EIDs, as well as being vulnerable to infection from novel human diseases in turn. This has resulted in the sharing of devastating pathogens to the detriment of both species (Wolfe, 1998). In particular, on the human side, the emergence and subsequent epidemics of Ebola (WHO Ebola Response Team 2015) and HIV (Hahn et al. 2000) has involved immense health, social and economic costs (Morens et al. 2004). As the relationship between humans and non-human primates alters as a result of human population growth and associated environmental change, the emergence of devastating zoonotic diseases involving parasites and pathogens is likely to become more pronounced. As such, a better understanding of the drivers of parasite transmission and occurrence in non-human primates may lead to better surveillance and management of potential EID risks to human populations.

Beyond the potential human zoonotic risk, specific attention should also be directed towards primate-parasite systems due to the fact that many primate species are facing extinction; ~60% of primate species are listed as threatened (classified as either Vulnerable, Endangered, or Critically Endangered) according to the IUCN Red List (Estrada et al., 2017). These species may be at further risk of decline from disease, particularly where they only persist in small populations (Smith et al. 2009). In addition, primates may be at increasing risk of parasitism and disease as a result of the anthropogenic threats they face (Chapman et al. 2005). Logging and land conversion are fragmenting non-human primate habitats, reducing food availability and increasing physiological stress, reducing genetic diversity and host condition, and increasing host density and contact rates as non-human primates gather in habitat fragments or begin crop raiding (Gillespie et al., 2005). Furthermore, global warming will shift the climate across the globe, altering primate behaviour, ecology, and the survival of their parasites (Guernier et al., 2004). All these factors have been associated with increases in parasite richness and prevalence in primate hosts (Chapman et al. 2005). Understanding primate-parasite ecology might help us identify the mechanisms responsible and thus help us to predict and mitigate against parasite-induced primate losses in the face of these future changes.

Baboons represent an ideal model system for studies into primate parasite ecology. There are six baboon species ranging across Africa and the Arabian Peninsula: *Papio anubis* (olive baboon); *Papio cynocephalus* (yellow baboon); *Papio hamadryas* (hamadryas baboon); *Papio kindae* (kinda baboon); *Papio papio* (Guinea baboon); and *Papio ursinus* (chacma baboon). Many baboon species are studied in long-term projects (e.g. study sites at Amboseli, Kenya;

and Gombe, Tanzania), and for this reason their behaviour and ecology have been, and continue to be, well documented. Part of their appeal is their accessibility. Baboons inhabit a range of environments, and populations of baboon are generally stable and extensive. In contrast to this, African ape populations are more restricted, exist at low densities and are at risk from human disease spread from observers (Wallis & Lee 1999), and so research into their health status in the wild can be a challenge. Some exploration into the similarity of parasites of baboons and sympatric primates have indicated that many baboon parasite species are shared with other primate species (McGrew et al., 1989; Murray et al., 2000). Therefore, baboons provide the opportunity to circumnavigate the challenges associated with studying infection levels in other, less easily studied, primate species. Additionally, baboons not only represent a phylogenetically similar parasite host to humans, but also live in close proximity to humans, increasing the likelihood of parasite transmission, and furthering their importance as a source of EIDs. Human-baboon contact rates are increasing in both urban (Hoffman & O'Riain, 2011) and agricultural landscapes (Hill, 2000), and increases in such contact rates have been associated with increased pathogen transmission (Drewe et al., 2012).

One limitation to studying infectious diseases in non-human primates is the need for clinical samples for quantifying infection. Helpfully, enteric parasites can be sampled non-invasively through faeces and are easily identified through inexpensive methods, i.e. light microscopy. For this reason gastrointestinal parasites, helminths, and protozoa, have been the focus of many host-parasite studies in baboons. Gastrointestinal parasites can be pathogenic and can cause severe parasitosis resulting in blood loss, diarrhoea, and tissue damage. However, others are considered commensals, where the detrimental effect on the host is indirect, reducing nutrient availability such that increased energy is required by the host to maintain its fitness (Coop & Holmes 1996). Gastrointestinal parasites also play a significant role in determining host survival, as noted in many wild animal populations (Tompkins & Begon 1999). For example, in Soay sheep (*Ovis aries*) population crashes have been associated with gastrointestinal parasites exacerbating the impact of nutritionally limited years, resulting in death from starvation (Gulland 1992). Their role as emerging infectious diseases is, however, limited. The mutation rate of infectious agents, and whether they are host generalists, is cited as a key determinant of whether they are at risk of emerging or re-emerging (Pedersen et al. 2005; Cleaveland et al. 2007). Viruses and bacteria are therefore considered to be of greater concern. Yet helminths and protozoa are emerging and re-emerging in human populations, for example *Cryptosporidium* spp., *Giardia* sp., and *Strongyloides* sp. (Woolhouse & Gowtage-

Sequeria 2005). Whilst gastrointestinal parasites are a potential source of EIDs, primarily gastrointestinal parasites are a model system for identifying general trends in parasite ecology.

In this contribution, I describe our current knowledge of baboon gastrointestinal parasites through a review of the literature. Specifically, I aim to: (1) quantify the prevalence of parasite species, identifying the most common baboon parasites, across Africa and the Arabian Peninsula; and (2) summarise what we know about potential individual-, troop-, and population-level predictors of variation in baboon parasite richness and abundance. Through this I hope to establish the role baboons play as hosts of zoonotic parasites and provide a resource summarising the findings from previous research. This will enable us to identify any gaps in the literature for future research priorities.

COMPILINING THE LITERATURE

I conducted a literature search with the purpose of collating all available records of gastrointestinal parasites across all baboon species in the wild. To search for these records I used a major online reference database (Web of Science), a primate-specific database (PrimateLit, primatelit.library.wisc.edu), and a mammal parasite database (Global Mammal Parasite Database, Nunn & Altizer 2005). I then located relevant records by using the genus name *Papio*. From this I compiled scientific articles and unpublished dissertations that had conducted a comprehensive screen for gastrointestinal parasite infections, i.e. where all parasite species found within the faecal samples were recorded. I therefore excluded any research that focused only on a specific parasite species (e.g. Deere et al. 2018; Müller-Graf et al. 1997; Weyher et al. 2010). Additionally, some publications were excluded as they provided no specific sampling location (Kuntz & Myers 1966; Munene et al. 1998; Muriuki et al. 1998; Goldsmid 1974; Kuntz & Moore 1973).

The resulting dataset covered 40 study sites (Fig. 2.1) drawn from 31 publications. Most studies were conducted on *Papio anubis* (olive baboon) and *Papio ursinus* (chacma baboon), contributing to 35% and 31% of the data respectively. *Papio hamadryas* (hamadryas baboon) made up 17%, *Papio cynocephalus* (yellow baboon) 10%, and *Papio papio* (Guinea baboon) only 5%. For *Papio kindae* (kinda baboon) I found no records of gastrointestinal parasites in the literature. The 40 study sites covered a diverse range of environments in Africa, from deserts (e.g. Kuiseb, Namibia) to rainforest (e.g. Gashaka, Nigeria). These also ranged from

highly seasonal environments, such as the high-latitude Cape Peninsula (South Africa), to the less seasonal equatorial, such as low-latitude Kibale (Uganda). The highest altitude site (above 2750m) was Giant's Castle in South Africa and the lowest altitude sites, near sea level (>0m), were Pringle Bay, South Africa, and Kilifi, Kenya.

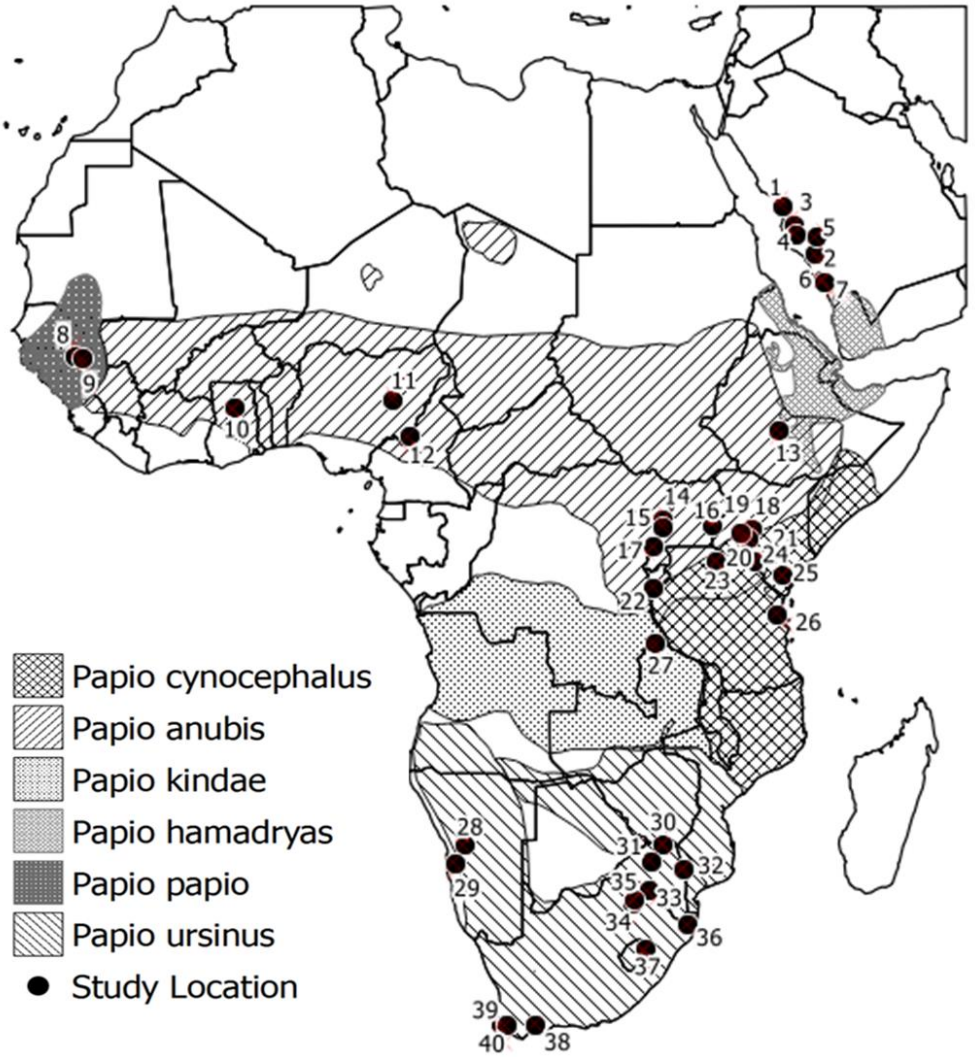


Figure 2.1: Baboon species distributions and locations of study sites. Baboon distribution data provided by IUCN (IUCN 2008). Study sites are [1] Al-Akhal (Ghandour et al., 1995); [2] Al-Baha (Ghandour, 1995); [3] Al-Rihat (Ghandour, 1995); [4] Al-Taif (Ghandour, 1995); [5] Turabah (Ghandour, 1995)); [6] Asir Highlands (Nasher, 1988); [7] Asir Lowlands (Nasher, 1988); [8] Mt. Assirik (Ebbert et al. 2013; McGrew et al. 1989); [9] Fongoli (Howells et al. 2011); [10] Mole National Park (Ryan et al. 2012); [11] Yankari National Park (Mafuyai et al. 2013); [12] Gashaka Gumti National Park (Weyher et al. 2006); [13] Rift Valley (Legesse & Erko, 2004); [14] Toro Game Reserve (Freeland, 1979); [15] Kibale National Park (Bezjian et al. 2008); [16] West Bugwe (Ocaido et al. 2003); [17] Bwindi (Hope et al. 2004); [18] Mpala Wildlife Research Centre (Hahn et al. 2003); [19] Mau Narok (Kuntz & Myers, 1967; Myers & Kuntz, 1968); [20] Gilgil (Eley et al. 1989); [21] Aberdares (Akinyi, 2017); [22] Gombe National Park (McGrew, 1989; Müller-Graf et al., 1996; Murray, 2000); [23] Amboseli National Park (Akinyi, 2017; Meade, 1984; Hahn et al. 2003); [24] Kimani (Kuntz & Myers, 1967; Myers & Kuntz, 1968); [25] Kilifi (Kuntz & Myers, 1967; Myers & Kuntz, 1968); [26] Saadani (Nonga et al. 2014); [27] Mahale National Park (Kooriyama et al. 2012); [28] Tsaobis Nature Park (Benavides et al. 2012); [29] Kuiseb (Appleton & Brain, 1995); [30] Scrutton Private Nature Reserve (Pettifer, 1984); [31] Limpopo (Goldsmid & Rogers, 1978); [32] Kruger National Park (McConnell et al. 1974); [33] Loskop Damn Nature Reserve (Pettifer, 1984); [34] Johannesburg (Myers et al. 1971); [35] Suikerbosrand Nature Reserve (Pettifer, 1984); [36] Mkuzi Game Reserve (Appleton et al. 1991); [37] Giant's Castle (Appleton et al. 1986; Appleton & Henzi, 1993); [38] Wildcliff (Ravasi et al. 2012a); [39] Cape Peninsula (Ravasi et al. 2012a); [40] Pringle Bay (Ravasi et al. 2012a).

GASTROINTESTINAL PARASITES OF BABOONS

Most studies assayed the presence and absence of parasites within a population through either faecal or post-mortem gastrointestinal samples. To identify the eggs and cysts in faeces, the samples were examined through light microscopy after concentrating the eggs and cysts from the faecal sample or through direct smears. Amoeboid parasites are identified through the morphology of encapsulated cysts, and helminth parasites are identified through the morphology of eggs. For both amoeba and helminth species identification can be compounded by the morphological similarity between species and therefore some publications recorded some parasite species to family level.

Using the data presented in these studies I extracted the presence of different parasite species for each population, identifying the most common baboon parasites across Africa and the Arabian Peninsula. The most ubiquitous protozoan and helminth parasite species across the 40 study sites are summarised in Tables 2.1 and 2.2 respectively. With respect to the protozoan parasites, the close morphological similarities of *Entamoeba* species means that some publications (15%) grouped these species into a single taxon. Nevertheless, across the remaining 85% of publications that did identify these amoebae to species level, the three most common protozoan parasites were *Entamoeba histolytica* (89% prevalence), *Entamoeba coli* (80%), and *Balantidium coli* (65%). These parasites were a mix of pathogenic and non-pathogenic species, but the common species are all transmissible to humans (Table 2.1). All the protozoan parasites are transmitted directly, either through the faecal-oral route, or as water- or food-borne pathogens. *Entamoeba histolytica* was the only pathogenic *Entamoeba* spp. reported, and along with *Balantidium coli*, is infectious to humans, New World monkeys, Old World monkeys, and apes (Abee et al., 2012). While *B. coli* is mostly asymptomatic, *E. histolytica* infection can result in disease, amoebiasis, which has been responsible for the deaths of multiple species including humans (Abee et al., 2012).

The helminth species reported varied in their transmission routes, with direct routes being those that rely on host-host or host-environment contact, and indirect routes being those that require an intermediate host. Some of the most prevalent helminths of baboons are transmissible to humans (Table 2.2). The three most common helminth species were the nematodes *Trichuris trichiura* (79%), *Physaloptera caucasia* (57%), and *Strongyloides* spp (57%). Both *Trichuris* sp. and *Strongyloides* spp. are transmitted from the soil via the faecal-oral route, and both are widely prevalent across human populations (Pearson, 2002).

Trichuris trichiura (whipworm) is found in the large intestine and caecum of many primate species: New World monkeys, Old World monkeys, and great apes (Abee et al., 2012). The adult worms of *T. trichiura* bury into the colon wall, and can cause abdominal pain, dysentery symptoms, and in extreme cases, death (Pearson, 2002). Identification of *Strongyloides* at the species level has indicated that *S. fuelleborni* (threadworm) is the most common infection seen in baboons, but *S. stercoralis* has also been identified (Obanda, 2015). Found in other Old World monkeys and great apes, this parasite infects the intestine which results in strongyloidiasis (Abee et al., 2012). Also found in humans, the morbidity caused by these infections is variable; low infections are generally asymptomatic but larvae can auto-infect their current host by visceral migration across the intestine and may damage the host's organs (Olsen et al., 2009; Abee et al., 2012).

Two helminth parasites that are highly prevalent across baboon populations, and many other primates, are the nematodes *Physaloptera* (= *Abbreviata*) *caucasia* and *Streptopharagus pigmentatus* of the order Spirurida (Table 2.2). *Streptopharagus pigmentatus* has been reported in multiple primate species: chimpanzees (*Pan troglodytes*); Japanese macaques (*Macaca fuscata*); long-tailed macaques (*Macaca fascicularis)*; samango monkeys (*Cercopithecus mitis*); vervet monkeys (*Cercopithecus aethiops*); red-tailed monkeys (*Cercopithecus ascanius*); and white-handed gibbons (*Hylobates lar*) (Nunn & Altizer, 2005). *Physaloptera caucasia* has been reported in chimpanzees (*P. troglodytes*); mandrills (*Mandrillus sphinx*); grivets (*Chlorocebus aethiops*); multiple guenons (*Cercopithecus albogularis*; *C. ascanius*; *C. mitis*; and *C. lhoesti*); red colobus (*Piliocolobus rufomitratus*); and mangabeys (*Cercocebus galeritus*) (Nunn & Altizer, 2005). Whilst this illustrates the range of primate species that may be infected with these Spirurida helminths, and the geographical reach of this parasite which spans Africa and Asia, this information should not be seen as a definitive list of hosts or locations. Both nematodes have an indirect lifecycle, requiring an invertebrate intermediate host for development and transmission. Whilst in Japanese macaques this transmission route is through coprophagous beetles (Machida et al., 1978). However, these routes are not definitive and might not be the exclusive transmission route, as both parasites have been observed in primate populations that do not consume coprophagous beetles (i.e. Tsaobis, Namibia: pers. obs.). Other species that have been identified as intermediate hosts of *Physaloptera caucasia* are either cockroaches (*Blatella germanica*: Petter, 1960) or locusts (*Schistocerca gregaria*: Poinar & Quentin, 1972). In fact, multiple intermediate host species may be important. When comparing the foraging habits of baboons Hahn et al. (2003) found conflicting patterns of abundance in these parasites:

troops feeding on provisioned resources had increased *P. caucasia* but decreased *S. pigmentatus* abundance compared to wild foraging troops. This may suggest that these parasite species transmit through different pathways.

FACTORS ASSOCIATED WITH BABOON PARASITES

Many of these studies explored the drivers of baboon parasite infection from broad scale patterns to increasingly fine resolution, namely the environment or population level, the social group level, and the individual host level. Here I summarise their findings (Table 2.3) and discuss selected aspects in more detail below.

Environmental/Population-level factors

Weather and seasonality

Benavides et al. (2012) found that parasite richness varied significantly across months and suggested the parasites showed seasonal trends. Parasite richness increased four weeks after temperature had increased and after rainfall events, which was mostly accounted for by changes in protozoan richness rather than changes in helminths. However, Akinyi (2017) found different patterns: increases in temperature were correlated with a reduction in parasite richness and the abundance of some parasites (*T. trichiura* and strongyles), whereas increases in rainfall showed no relationship with parasite abundance except in the reduction of two helminth species (*T. trichiura*, and *P. caucasia*). Ravasi et al. (2012a) reported that helminth richness differed across years, but this was not the case for protozoan richness, and that *Trichostrongylus* sp. and *Trichuris* sp. egg outputs were seasonally fluctuating. However, this was troop dependent and was the only seasonal pattern observed across all the parasites in the community they studied (Ravasi et al., 2012a). Pettifer (1984) compared parasites between the dry and wet seasons and found that the associations were parasite species-dependent: *P. caucasia* and *S. pigmentatus* did not vary seasonally (as seen in Benavides et al., 2012), whereas *Trichostrongylus* sp. were more abundant during the dry season, and *Bertiella studeri* and *Oesophagostomum bifurcum* were more abundant during the wet season.

Social group level factors

Troop size and ranging behaviours

Although troop size has been hypothesised to be related to parasite richness in primates more generally (Freeland, 1979; McGrew et al., 1989) this correlation was not significant in any of the baboon studies reported here (Ravasi, 2009; Müller-Graf et al., 1996). The density of populations and home range size were also not significant factors in parasite richness or prevalence (Ravasi, 2009; Benavides et al., 2012; Müller-Graf et al., 1996). Nevertheless, some movement behaviours have been reported as being associated with variation in parasite richness, with increased troop overlap associated with increasing protozoan richness and *Trichostrongylus* sp. abundance (Ravasi, 2009), and longer daily distance travelled correlating with increased parasite richness (Benavides et al., 2012b).

Home range quality: altitude and proximity to humans

Papers reporting differences in parasite communities between baboon troops often attribute these differences to variation in food availability (Hahn et al., 2003; Weyher et al., 2006; Meade, 1984; Eley et al., 1989). The differences in food consumed by the troops might be due to variation in home range quality, or the troop's proximity to human settlements. Appleton et al. (1991) and Appleton and Henzi (1993) found that at low altitudes there was a higher diversity of parasite species, but lower egg outputs. They observed that troops at higher altitudes spent longer foraging and travelled further for food, possibly due to the food's low nutritional value, and suggested that the nutritional stress changed the host's susceptibility to parasite infection (Appleton & Henzi, 1993). Another possibility was that the foods consumed at the higher altitude were more likely to involve plant matter in the soil where parasites may be persisting (Appleton & Henzi, 1993). Proximity to human settlements has also been reported to result in notable differences in parasite abundance for all parasite species (Ocaido et al., 2003; Weyher et al., 2006; Ghandour, 1995), or for particular parasite species (e.g., Strongyles: Eley et al., 1989; *Physaloptera* sp. and *Streptopharagus* sp.: Hahn et al., 2003; *Physaloptera* sp., *Trichuris* sp., and *B. coli*: Weyher et al., 2006). However, Ravasi (2009) found no association between parasite prevalence and the consumption of human-derived foods in baboons in South Africa. Overall, there may be multiple routes by which natural and anthropogenic resource availability can influence transmission: it may alter the host's exposure to the parasites (e.g. changes in the distances travelled), or the host's susceptibility to infection (e.g. the nutritional benefit of human food enable better immune responses).

Individual host factors

Age

In multiple studies a non-linear, polynomial, relationship between age and parasites were observed. Pettifer (1984) noted that parasite abundance increased with host age, until a point, after which it started to decrease. This pattern was supported by Benavides et al. (2012), where a polynomial relationship between age and parasite richness was found. Similarly, Ravasi (2009) found that many parasite species are more abundant in adults than juveniles. However, some studies had found no correlation between age and parasite prevalence or richness, but noted that age-related patterns in abundance varied depending on the parasite species (Meade, 1984; Müller-Graf et al., 1996; Akinyi, 2017).

Sex and reproductive status

Most studies reported no differences in parasite prevalence (Ryan et al., 2012; Ravasi, 2009) or parasite species abundance (Meade, 1984; Müller-Graf et al., 1996; Pettifer, 1984) between male and female baboons. However, some parasite species seem to be an exception; *S. pigmentatus* was more abundant in female than males (Müller-Graf et al., 1996), and *P. caucasia* was more abundant in males at one site (Pettifer, 1984) but more abundant in female baboons at another site (Meade, 1984). Overall, Benavides et al. (2012) found parasite richness was higher in females than in males. Reproductive status had been reported as a correlate of parasite intensity for some species, e.g. *P. caucasia* and *S. pigmentatus* increased in pregnant females (Akinyi, 2017), while conflicting results showed *T. trichiura* egg output either increased in lactating females (Müller-Graf et al., 1996), or was no different across reproductive states (Ravasi, 2009).

Body condition

Many papers have alluded to the importance of host body condition in influencing gastrointestinal parasite communities in baboons (Appleton & Henzi 1993; Hahn et al. 2003; Weyher et al. 2006; Meade 1984). At the population level, Eley et al. (1989) observed that troops with lower body fat and body weight were more prone to parasites, with higher abundances seen in troops of lower condition. At a higher resolution, within troops, Benavides et al. (2012) and Akinyi (2017) both found that individual body condition (derived from skin-fold thicknesses and body mass indices respectively) was negatively associated with parasite richness, i.e. animals in better condition were infected with fewer parasite species. Akinyi (2017) attempted to explore the physiology behind the individual variation in

condition and parasites but observed no relationship between red blood cell indices (packed cell volume and other indicators of anaemia) and parasite richness.

Dominance

Most research has found no relationship between parasite richness or abundance and the dominance rank of individual baboons (Ravasi 2009; Benavides et al. 2012; Müller-Graf et al. 1996), except that Ravasi (2009) observed the prevalence of Trichostrongylus sp. was positively correlated with the rank of female baboons, i.e. females of higher rank had fewer parasite eggs. Conversely, Meade (1984) found that parasite abundance was related to the hierarchy position only for male baboons.

Table 2.1: Common protozoan parasites of baboons

Phylum	Family	Species	% Study sites present	Transmission	Morbidity / Mortality	Evidence in humans?	References
Archamoeba	Entamoebidae	*Entamoeba histolytica*	89	Direct	Amoebiasis, death	Yes	[1]; [5]
		Entamoeba coli	80	Direct	Asymptomatic	Yes	[1]
		Iodamoeba buetschlii	51	Direct	Asymptomatic	Yes	[1]; [5]
		Entamoeba hartmanni	37	Direct	Asymptomatic	Yes	[1]
		Entamoeba nana	30	Direct	Asymptomatic	Yes	[1]
Ciliophora	Balantiidae	*Balantidium coli*	65	Direct	Balantidiasis, death	Yes	[2] [3]
Sarcomastigophora	Heamitidae	*Giardia* (=*lamblia*, *intestinalis*, *duodenalis*)	43	Direct	Giardiasis, diarrhea	Yes	[4]
Metamonada	Retortamonadida	*Chilomastix mesnili*	29	Direct	Asymptomatic	Yes	[4]

Parasitic protozoa reported in >20% of study sites. The order of parasite species and phylum is reflective of the most prevalent parasite species. Where the name of a species is followed by (=), these are the alternative names that are also present in the literature. The species have been ordered alphabetically. [1] Martínez-Palomo 1993; [2] Zaman 1993; [3] Schuster & Ramirez-Avila 2008; [4] Kreier & Baker 2012; [5] Abee et al. 2012

Table 2.2: Common helminth parasites of baboons

Phylum	Family	Species	% Study sites present	Transmission	Morbidity / Mortality	Evidence in humans?	References
Nematoda	Trichuridae	*Trichuris trichiura*	79	Direct	Asymptomatic, lethagy, diarrhea	Yes	[1]; [2]
	Physalopteridae	*Physaloptera* (=*Abbreviatta*) *caucasica* (=*caucasia*)	57	Indirect	Unknown	No	[2]
	Strongyloididae	*Strongyliodes* spp (=*fulleborni* or *fuelleborni*)	57	Direct via free-living	Diarrhea, death	Yes	[2]
		Strongyles*	26	N/A*	N/A*	N/A*	
	Strongyloidae	*Oesophagostomum bifurcum*	48	Direct	Asymptomatic, lethagy, diarrhea	Yes	[2]
	Spirocercidae	*Streptopharagus pigmentatus*	45	Indirect	Unknown, death	No	[2]
	Trichostrongylidae	*Trichostrongylus* spp (=*falculatus*)	40	Direct	Unknown	No	[2]
	Hookworms (general)	N/A*	36	N/A**	N/A**	N/A**	
	Oxyuridae	*Enterobius* (=*Oxyuris*) *vermicularis*	35	Direct	Irritation	Yes	[1]; [2]
	Ascarididae	*Ascaris* spp (=*lumbricoides*)	24	Direct	Asymptomatic, deaths reported	Yes	[1]; [2]
Platyhelminths	Anoplocephalidae	*Bertiella studeri*	31	Indirect	Abdominal pain	Yes	[2]
	Schistosomatidae	*Schistosoma mansoni*	24	Indirect	Asymptomatic	Yes	[1]; [2]

Parasitic helminths reported in >20% of study sites. The order of parasite species and phylum is reflective of the most prevalent parasite species. Where the name of a species is followed by (=), these are the alternative names that are also present in the literature. [1] Bogitsh et al. 2005; [2] Abee et al. 2012

*Strongyles are a general term for multiple species, which have not been identified to species level in the publications**Hookworms are a general term form multiple species, and many papers did not identify to species level. Common species include *Ancylostoma* sp. and *Necator* sp., both are infectious to humans and directly transmitted [2]

Table 2.3: Summary of findings for different drivers of baboon parasitism across studies

Baboon Species	Study site	Parasite Metric	Environment				Social factors			Individual					Refs
			Season	Temp	Rainfall	Troop size	Ranging patterns	Urban	Altitude	Age	Sex	Reproductive state	Body Condition	Dominance	
P. anubis	Gashaka Gumti NP, Nigeria	Multiple						–			o				[1]
P. anubis	Gilgil, Kenya	Abundance						–		o	o				[2]
P. anubis	Gombe NP, Tanzania	Multiple									o*	+ (lactating)		o	[3]
P. anubis	Mole NP, Ghana	Prevalence									o				[4]
P. cynocephalus	Amboseli NP, Kenya	Abundance		–	–	+				+		+ (pregnant)	–	o	[5]
P. cynocephalus	Amboseli NP, Kenya	Abundance	X							–	o	+ (pregnant)		+ (males)	[6]
P. hamadryas	*multiple*, Saudi Arabia	Prevalence		+											[7]
P. ursinus	Giant's Castle, South Africa	Abundance							–						[8]
P. ursinus	Mkuzi GR, South Africa	Abundance							–						[9]
P. ursinus	*multiple*, South Africa	Abundance			+/-					+/-	o*				[10]
P. ursinus	*multiple*, South Africa	Prevalence	X*		–*	o	– (range overlap)			+	o	o		o (females)	[11]
P. ursinus	Tsaobis NaP, Namibia	Richness	X	+	+		+ (travel distance)			+/-	+ (females)		–	o	[12]

Variables associated with parasite abundance, richness, and/or prevalence: + indicates a positive correlation with that variable, - indicates a negative correlation, o indicates no relationship, and a blank space indicates that driver was not tested. * indicates that effects were not seen for all parasites, but there may be some parasite species-specific correlations. [1] Weyher et al., 2006; [2] Eley et al., 1989; [3] Müller-Graf et al., 1996; [4] Ryan et al., 2012; [5] Akinyi, 2017; [6] Meade, 1984; [7] Ghandour et al., 1995; [8] Appleton & Henzi, 1993; [9] Appleton et al., 1991; [10] Pettifer, 1984; [11] Ravasi, 2009; [12] Benavides et al., 2012. NP = National Park; GR = Game reserve; NaP = Nature Park

DISCUSSION

Baboons are a valuable system for exploring parasite ecology by being a model for human and non-human primate parasites. Here I have collated data to determine the prevalence of parasite species across baboon species and populations and reviewed what we know about the potential drivers of the patterns of parasite prevalence, and species abundance and richness. I will now consider how these patterns compare with those found in other primate taxa and consider the potential for zoonotic transmission between baboons and humans.

Drivers of parasite infection

Our review of studies exploring the drivers of parasite prevalence and abundance indicates a great deal of variation in the findings. Much of this variation may reflect biological differences between populations, such as the host species, parasite community, and local environment (its seasonality and climate), as well as methodological differences between studies, such as the period of study, the number of individuals and troops assessed, and the methods of faecal analysis adopted. Nevertheless, some consistent patterns did emerge. In particular, seasonality appeared to have an important influence wherever it was assessed, whereas individual sex and dominance rarely had an effect. Here I discuss key aspects of these findings in more detail.

With respect to age, most studies reported either a positive correlation between age and parasite abundance (Akinyi, 2017; Ravasi, 2009), or a polynomial relationship, increasing with age until a threshold after which parasites decrease with age (Benavides et al., 2012; Ravasi, 2009). The former pattern follows the hypothesis that hosts accumulate parasites over time through a stable probability of encountering parasites (Nunn & Altizer, 2006). In contrast, the polynomial patterns may arise as the result of immunity development as the host repeatedly contacts parasites, such that their susceptibility to parasites decreases over time (Hudson & Dobson, 1997). This concave age-infection curve has been observed across many different systems: *Schistosoma mansoni* in snails (Anderson et al., 1982) and humans (Woolhouse et al., 1994); helminths in Japanese macaques (*M. fuscata yakui*: MacIntosh et al., 2010); and helminths in rabbits (*Oryctolagus cuniculus*: Cattadori et al., 2008). However, MacIntosh et al. (2010) and Boag et al. (2001) noted that age-abundance trends can be parasite species-dependent in both Japanese macaque and rabbit systems. For example, macaque parasites transmitted using an intermediate host (*Streptopharagus* sp. and *Gongylonema* sp.) follow a

convex trend (MacIntosh et al., 2010). Whilst the concave relationship is seen across much of the literature, the drop-off in parasite abundance in older individuals might be due to biased sampling: fewer individuals in the older age classes results in a reduced sampling effort, and smaller sample sizes often underestimate the abundance or prevalence of parasites within a group (Wilson et al., 2001).

Male and female baboons rarely showed a difference in their abundance/intensity or prevalence of parasitism. This contrasts with our expectation, as previous meta-analyses have found that male mammals typically harbour higher infections of parasites than females for both helminths and protozoa (Poulin, 1996; Schalk & Forbes, 1997). There are several hypotheses surrounding which physiological or behavioural differences might drive this disparity (Zuk & McKean, 1996). In particular, hormones are often considered to play a role due to testosterone's immunosuppressant effects (Grossman, 1985). This is supported in part by Schalk & Forbes' (1997) observation that the differences between the sexes only arose in adult hosts and not in juveniles. Nevertheless, only one difference in parasite richness between males and females was observed in the literature that I reviewed, indicating that females had a higher richness of parasites than males (Benavides et al., 2012). A few other studies also reported sex differences between the abundance of specific parasite species: Müller-Graf et al. (1996) found females carried more *S. pigmentatus* and Pettifer (1984) found males carried more *P. caucasia*. Both these parasites are transmitted by invertebrate intermediate hosts, of which Meade (1984) reports that females consume more invertebrates than males do. Yet Pettifer (1984) suggests that if foraging differences were a driver for sex differences in parasite abundance, the pattern would be seen for both *S. pigmentatus* and *P. caucasia* as they are transmitted through the same route. Generally, for most parasites there is little evidence of male and female baboons carrying a higher abundance of infection, and some evidence of differences in parasite richness has been observed. Poulin (1996) suggests that these patterns between host sex and parasites can be subtle and difficult to observe in the wild, so it might require finer-resolution studies to observe these effects in baboons.

An influence of hormones on parasite burdens might explain the correlation between male dominance and parasites seen by Meade (1984). In chimpanzees (*P. troglodytes schweinfurthii*) higher testosterone levels, associated with higher position in the dominance hierarchy, were positively correlated with helminth burdens (Muehlenbein & Watts, 2010). In mandrills (*M. sphinx*), however, there were no associations between rank and parasite

abundance (Setchell et al., 2007). Apart from Meade (1984), no other articles found an association between baboon rank and parasite prevalence (Ravasi, 2009), abundance (Akinyi, 2017; Müller-Graf et al., 1996), or richness (Benavides et al., 2012). In Japanese macaques associations between dominance and parasite abundance are species dependent: *Oesophagostomum* sp. is negatively associated with female rank, but no association is seen with *Streptopharagus* sp. (Hernandez et al., 2009). Whilst the physiological aspects of dominance rank are often cited as a driver in parasite trends, behavioural rank differences are more complicated. In Japanese macaques dominance rank altered locomotion and foraging habits (MacIntosh et al., 2011). These behavioural variations between individuals may result in a difference in their exposure to parasites, where higher ranking individuals may secure better resources away from areas with more parasites (Nunn, 2006a). Or these behavioural differences may result in increased body condition through dominant individuals accessing higher quality foods, and hence improve their ability to resist infection through better immunocompetence (Nunn, 2006a). With many potential mechanisms driving associations between social rank and parasite infection, it may be difficult to disentangle the effects through correlations alone.

The two studies that assessed baboon body condition and parasitism found a negative correlation: as host condition declined, parasite richness/abundance increased (Akinyi, 2017; Benavides et al., 2012). The association of gastrointestinal parasite infection and body condition has been seen in multiple host-parasite systems, e.g. in Soay sheep, strongyles and coccidia were negatively associated with body weight (Craig et al., 2008). However, identifying cause and effect is problematic, and this is often seen as cyclic and without a definitive answer as to which precedes the other (Beldomenico & Begon, 2010). Reduced condition of a host is detrimental to its ability to fight against infection, leading to more infections, and that in turn results in reduced condition. The only way to untangle these relationships is through experimental studies. Removal of ectoparasites from ground squirrels (*Spermophilus columbianus*) saw an increase in body condition (Neuhaus, 2003). Similarly, domestic chickens with experimentally removed helminth parasites were seen to have increased growth rates compared to those that were infected (Katoch et al., 2012). A review of the nutritional health of ruminants and their subsequent ability to resist gastrointestinal parasites found that diet influenced the establishment of adult helminths (van Houtert & Sykes, 1996). Interestingly, in reindeer (*Rangifer tarandus tarandus*) gastrointestinal parasite infection altered host behaviour, reducing food intake when the parasite burdens were high compared to individuals with their gastrointestinal parasites

removed (Arneberg et al., 1996). It is therefore likely that multiple mechanisms are shaping the relationship between baboon condition and parasite abundance, especially when increased nutrition is associated with supplementation from human sources (Becker et al., 2015).

In baboons there is some evidence of troop traits, such as group size or ranging behaviours, being associated with parasite abundance, prevalence, and richness. Troop size was positively association with parasite abundance (Akinyi, 2017). This pattern has been reported across multiple taxa in a meta-analysis finding a weak tendency for larger groups to harbour more parasites, regardless of the transmission mode of the pathogen (Rifkin et al., 2012). In primates, however, meta-analyses have found less consistent results, when phylogeny is accounted for then the effects of group size fall away, and instead population density is a strong predictor of helminth and protozoal richness (Nunn et al., 2003). From a meta-analysis across social mammals Côté & Poulin (1995) noted these patterns generally hold true only for directly transmitted parasites (i.e. via social or environmental contact), but the opposite effect was observed for those mediated by an intermediate host. Further work into the relationship of baboon troop size and parasite richness should explore this relationship in context of the transmission routes of the parasites.

Potential for zoonotic transmission

The literature on baboon parasites has shown that many of their parasites are generalists, capable of infecting other primate species, including humans. This deviates from the expectation that helminths are more host specific, indicating that gastrointestinal parasites may emerge or re-emerge into primate populations (Cleaveland, 2007) and have the potential to be zoonotically transmitted to humans.

Baboons carry some of the world's neglected tropical diseases, including soil transmitted helminths (Pullan et al., 2014), and *Schistosoma mansoni* (Colley et al., 2014). The soil-transmitted helminths such as *Trichuris* sp. (whipworms), hookworms, and *Ascaris* sp. (roundworms) are significant contributors to global ill health, with a combined estimated DALYs (disability-adjusted life years) loss of 2.86 million years in 2002 (Feasey et al., 2010). The estimated global incidence of soil transmitted helminths was 1.45 billion people in 2010 (hookworm = 439 million; *Ascaris lumbricoides* = 819 million; and *T. trichiura* = 460 million: Pullan et al., 2014), and the global impact of these parasites is significant, with the economic

burden of hookworm alone estimated to be between $2.5 billion - $138.9 billion (Bartsch et al., 2016). The extent to which these parasites may be derived from non-human parasites is currently unclear. Molecular techniques have started to uncover the relationship of the different *Trichuris* subtypes which can help us to determine whether transmission occurs between humans and non-human primates (Hawash et al., 2015). Ravasi et al. (2012b) observed that *Trichuris* sp. were molecularly similar between humans and non-human primates. The fact that many baboon parasites have zoonotic potential has been a key finding of many papers recording the gastrointestinal parasites of baboons. For example, Nasher (1988), Ocaido et al. (2003), and Meade (1984) all observed that the same parasite communities were present in humans that lived in close proximity to their sampled baboon population.

Baboons are also host to several protozoa known to cause diarrhoea in humans: *E. histolytica*, *B. coli*, and *Giardia* sp.. Their impact on humans can be significant. In the first case, although there are several morphologically similar *Entamoeba* species only one is considered pathogenic: *Entamoeba histolytica* (Shirley et al., 2018). Diarrhoea from amoebiasis (*E. histolytica* infections) was responsible for >55,000 human deaths in 2010 and is the third leading cause of death in young children across the globe (Lozano et al., 2012; WHO, 2002). However, the reporting of this parasite in baboons might be overestimated, as *E. histolytica* is identical to *Entamoeba dispar*. There is also some discussion as to whether *E. histolytica* in baboons has been misidentified as the morphologically identical *Entamoeba nuttalli* (Elsheikha et al., 2018). To add to this confusion *E. nuttalli* has been observed to transmit between non-human primates and humans (Levecke et al., 2015). In the second case, *B. coli* is a large ciliated protozoan infecting many Old World primates (Muriuki et al., 1998; see also, mandrills: Poirotte et al., 2017), and humans (Schuster & Ramirez-Avila, 2008). This ciliate consumes nutrients passing through the colon (Schuster & Ramirez-Avila, 2008), reducing the nutrients available to its host. Infections with *B. coli* in humans might not necessarily result in balantidiasis, the associated ulcerative disease (Schuster & Ramirez-Avila, 2008), but if it does then the symptoms are diarrhoea or dysentery (Vázquez & Vidal, 1999). All the *Entamoeba* species recorded in Table 2.1 are also parasites/commensals of humans (Sodeman, 1996; Ali, 2015). In the third case, *Giardia* sp. and *Cryptosporidium* sp. have both been reported in baboons, although at a low prevalence (Table 2.1, and *Cryptosporidium* sp. only reported in <6% of study sites). These parasites cause giardiasis and cryptosporidiosis in humans (Kreier, 2012), respectively, but are difficult to identify through microscopy and may have been underreported in these baboon populations.

Methodological considerations

In this review, faecal egg counts have been equated with parasite infection (i.e. parasite abundance or intensity). Although this reflects the approach adopted in the original papers, it is worth noting that faecal samples only show parasite output (cyst or egg emissions) (Gillespie, 2006). Parasite egg and cyst production is often used as a reflection of infection intensity, and in some cases it has been shown that these counts correlate well with internal worm abundance (Seivwright et al., 2004). However, none of these baboon studies, including those conducted post-mortem, have correlated egg output with worm biomass. The only exception is that of Kuntz and Moore (1973), who noted that *Bertiella* sp. prevalence is lower when determined from faecal samples compared to autopsy observations. Additionally, protozoan parasites replicate within the host, making their outputs a reflection of their ability to reproduce rather than their relative burdens (Anderson & May, 1978b). Therefore, I suggest that the results of these studies are interpreted with caution, especially in terms of inferring infection burdens. Nevertheless, the faecal egg counts do indicate parasite presence and transmission potential.

In addition, it is often assumed that the presence of morphologically similar parasites in humans living alongside baboons indicates that zoonotic transmission is occurring. This inference is supported by the observation that antibiotic-resistant bacteria are more prevalent in baboons living close to humans (Rolland et al., 1985), and by reports of tourists and scientists becoming infected by parasites present in local baboon populations (Fenwick, 1969; Hasegawa et al., 2010). However, the inference of parasite host-sharing through morphological identification of the eggs and cysts present in the faeces can be unreliable, as different parasite subspecies may be morphologically similar but circulate independently in each host species ('cryptic specificity': (Withenshaw et al., 2016)). Consequently molecular techniques are necessary to confirm if cross-species transmission is taking place. For instance, studies of the molecular similarity between the *O. bifurcum* infecting baboons and humans in Togo and Ghana have indicated that transmission occurs solely within the host species and therefore the parasite is not transmitted between humans and non-human primates (Gasser et al., 2006; Van Lieshout et al., 2005). In other host-parasite systems, molecular identification has revealed parasites that, although carried by two host species, are actually host-specific variants: e.g. *Bartonella* sp. in wood mice (*Apodemus sylvaticus*) and bank voles (*Myodes glareolus*) (Withenshaw et al., 2016). Such studies emphasise the

need for detailed molecular diagnostics to confirm or refute the existence of potential cross-species transmission pathways. Even when molecular studies have supported the zoonotic transmission of gastrointestinal parasites (*Cryptosporidium* sp. and other protists: Li et al., 2011 and Parsons et al., 2015; *Trichuris* sp.: Ravasi et al., 2012b; *Giardia* sp.: Levecke et al., 2009) the direction of transmission between humans and baboons is generally unconfirmed. Hopefully further molecular studies will enable confirmation of zoonotic transmission.

CONCLUSION

Here I have provided an overview of the gastrointestinal parasites of baboons, their diversity, and drivers. I have also illustrated their importance for studies into zoonotic gastrointestinal parasites more generally, both due to the potential risk they pose as an emerging infectious disease and for their utility as a model for other host-parasite systems. However, despite the numerous studies to date, further research is necessary to fully assess the patterns of parasitism across all baboon species. In particular, *P. kindae* are not represented, and there are geographic limitations to where sampling has occurred, especially for *P. hamadryas* which is only represented on the Arabian Peninsula. Further work into the transmission routes of baboon parasites, especially using molecular analysis, would also provide valuable insight into whether these parasites are transmitted to humans, and vice versa.

CHAPTER THREE

Macroecological variation in baboon gastrointestinal parasite communities: patterns and processes

ABSTRACT

The gastrointestinal parasite community varies within and between baboon species. In an attempt to understand this variation, I explored patterns of helminth community composition reported in the literature across 40 populations encompassing five baboon species across Africa and the Arabian Peninsula. I found that helminth parasite communities are independent of baboon species or phylogeny with the exception of the Arabian *P. hamadryas*, which is differentiated from all other species. Unexpectedly, baboon populations that were more distant from one another had more similar helminth communities. Local vegetation greenness (indexed by NDVI, the normalised difference vegetation index) and/or rainfall were important predictors of helminth community composition and richness, and were also identified as possible drivers of individual parasite species occurrence (helminths: *Oesophagostomum* sp., *Streptopharagus* sp., *Trichuris* sp.; protozoans: *Balantidium* sp.). However, the effects of NDVI and rainfall in these latter models were inconclusive. Overall, these results suggest that variation in gastrointestinal parasites within and between baboon species is more strongly driven by local environment than by host species identity, but more work is required to confirm which environmental variables are most important and the mechanisms through which they operate.

INTRODUCTION

Understanding how parasite community composition varies within and between host species can provide valuable insights into the evolution of host-parasite relationships (Pedersen & Fenton, 2007). In addition, such understanding may prove invaluable as anthropogenic environmental change affects the life cycle and transmission of parasites, driving the emergence and re-emergence of infectious diseases (Altizer et al., 2013; Daszak, 2000; Harvell et al., 2002; Pounds et al., 2006) or resulting in the decline of parasites with concomitant effects on the host and wider ecosystem (Rohr et al., 2011). The identification of which factors underpin parasite community composition, and understanding how these factors will shift as the environment changes, will be key to predicting and developing appropriate management responses to these future events.

There are several potential factors that may contribute to variation in parasite community composition. To begin with, the host specificity of the parasite and the spatial proximity of

its potential hosts are important determinants of a parasite's ability to infect multiple hosts (Cleaveland et al., 2001; Davies, 2008; Poulin & Morand, 2000).

In the first case, the host specificity of a parasite is inversely proportional to the number of host species it can infect, with those of low specificity, i.e. host generalists, considered to pose the greater risk for emerging infectious diseases (Cleaveland, 2001), irrespective of the route of transmission (Jones et al. 2008; Taylor et al. 2001). Whether a parasite is a host specialist or generalist is shaped by the way it trades off the benefits of adaptation to the host immune response versus the benefits of opportunistically exploiting and colonising new hosts. These differences in host specificity are seen to different degrees across parasite types, with viruses and protozoa being less host specific than helminths (Cleaveland, 2001; Cooper et al., 2012; Nunn et al., 2004; Pedersen, 2005). The occurrence of a parasite in two different species may come about through two different routes: common ancestry and host colonisation (Page, 1993; Poulin, 2000), although the latter may still favour more closely related species as it relies on the ability of a parasite to be preadapted to a particular host trait (Agosta et al. 2010). This suggests an important role of evolutionary history, and indeed, the phylogenetic distance of primate clades has been associated with the similarity of their helminth communities (Cooper et al. 2012; Davies & Pedersen 2008; Nunn et al. 2004). Nevertheless, evolutionary history fails to explain all the patterns of parasite sharing seen in primates (Cooper, 2012; Nunn, 2003). Rather, host ecological traits also shape the parasite community, including the host's geographical range (Cooper, 2012), ranging behaviour (Nunn, 2003), similarity of host physiology to other hosts (Lindenfors et al. 2007; Poulin & Morand 2000; Vitone et al. 2004) and group size.

In the second case, communities in closer proximity to one another tend to be more similar than those further away, a pattern well known in biogeography as distance decay (Nekola, 2007). Environmental similarity decreases along a gradient, consequently, the distance-decay of species similarity may be a response to a decline in favourable environmental conditions (Koleff et al., 2003; Nekola, 2007). Another mechanism that might contribute to distance decay is physical geographical boundaries, including physically limited habitats, and the intrinsic inability of a species to disperse across that boundary (Warburton et al., 2016). Nevertheless, for parasites, geographic distribution is dependent not only on the ability of the parasite to extend its range across environmental conditions but also the availability and dispersal of suitable hosts. This may help to explain why a growing number of studies have failed to find distance decay in parasite communities (Pérez-Del-Olmo et al., 2009). In bats,

intestinal helminth communities were shaped by environmental conditions rather than geographical patterns (Warburton, 2016). Likewise, ectoparasite communities on small mammals were influenced by the environment rather than the spatial differences in host fauna (Vinarski et al., 2007). Yet in a meta-analysis of the distance-decay of helminth communities, the pattern was seen in some host systems (Poulin, 2003). This suggests that understanding distance decay patterns can help to illuminate the underlying factors that drive parasite community composition.

Baboons (genus *Papio*) provide an ideal taxon in which to explore the processes driving parasite community composition: the genus contains five species, allowing us to investigate the influence of host phylogenetic similarity on parasites, and these species have been studied over multiple populations, allowing us to assess the potential role of distance decay. In addition, baboons have another advantage relating to a further factor that can influence parasite community composition (highlighted in several of the studies cited above), namely the local environment. Baboon populations are widely distributed across latitudes, altitudes and environments (from desert to rainforest, and from coastal fynbos to montane habitats), allowing a robust analysis of environmental effects.

Previous population-level research into variation in baboon parasite communities has identified several possible environmental drivers (See previous chapter, Table 2.3). Temperature, precipitation, altitude, and proximity to humans have all been associated with baboon parasites, along with seasonal fluctuations (Benavides, 2012; McGrew, 1989; Meade, 1984; Ravasi, 2012). Such associations are generally supported by other primate studies (Nunn, 2006a).

Temperature is likely to influence parasite survival and development in the life-cycle stages outside of the host, and will influence intermediate host populations (Dobson & Carper, 1992a; Nunn, 2006a). Whilst higher temperatures are often assumed to increase parasite survival (Nunn, 2006a), the opposite might also be true. For example, Appleton & Brain (1995) observed lower parasite diversity in desert-dwelling baboons, and pointed to the harsh climate as a determinant of this pattern. Precipitation has a variable association with baboon parasites at a population level, with some relationships being positive (Benavides et al. 2012a; Pettifer 1984), and some negative (Akinyi, 2017; Pettifer, 1984; Ravasi, 2009). Theoretically, the development of parasites in response to rainfall events, or continuing damp conditions, should enable parasite survival and replication (Nunn, 2006a), but high

levels of rainfall might equally wash faecal matter and parasites away from the ranging locations of a troop (Freeland, 1980). The effects of temperature and rainfall may also be mediated indirectly through vegetation and host behaviour. In the first case, vegetation may be important for parasite survival through its role in creating microhabitats with optimal thermal and moisture conditions (Bavia et al., 2001; Ceccato et al., 2005). The extent of vegetation is also likely to reflect host food availability with effects on both the health and movement behaviour of the host (Pebsworth et al., 2012). This leads on to the second case, host behaviour, and in particular ranging patterns, which are expected to alter the host's probability of encountering parasites (Nunn, 2006a). Temperature is a limiting factor in baboon movement and habitat use (Hill, 2006) and at a continental-wide level, baboon movement behaviour is driven by rainfall and temperature (Johnson et al., 2015a). Unsurprisingly, the ranging behaviour of baboon troops has been associated with parasite richness in some populations (Benavides et al., 2012; Ravasi, 2009).

Proximity to human settlements is a further potential influence on baboon parasite communities, especially where this provides access to human foods and food waste. Human foods differ from wild foods based on their high nutrient content and the clustered locations of where they occur (e.g. tourist sites, landfills, agricultural crops). There are multiple mechanisms through which these 'provisioned' foods might influence parasites, some of which can potentially result in contradictory impacts, with meta-analyses used to try and untangle the dominant effects (see Becker et al., 2015). Hosts might well benefit from provisioning, increasing nutrition which may supplement the high cost of immune defences against parasites (Nunn, 2006a). The movement behaviour of the host may also be altered, either through the clustered resources increasing contacts between hosts, or the nutritional benefits shifting the activity budgets away from travelling and foraging (Altizer et al., 2018; Altmann & Muruth, 1988; Nunn et al., 2011). *Papio* species are particularly prone to increased infections in a provisioned habitat due to their larger home ranges and generalist diet (Becker et al., 2018). This was particularly pronounced for protozoa infections but was also important for helminth infections in *Papio cynocephalus*.

A further environmental factor that can influence parasite communities, but has not previously been explored in baboons, is latitude. Latitude is one of the main predictors of free-living species biodiversity, a pattern usually attributed to environmental gradients associated with productivity (Hawkins et al. 2003; Rohde 1992; Gillman et al. 2015; Gaston 2000; Willig et al. 2003). As a rule, the richness (number) of plant and animal species per unit

area increases towards the equator. The expectation for parasites is that they should follow a similar pattern: parasite richness is coupled with the richness of host species, and therefore parasite diversity should increase along the latitudinal gradient too. Despite this expectation, meta-analyses exploring this association have had mixed results. Some studies have reported a positive relationship, including helminths in carnivores (Lindenfors et al., 2007) and ectoparasites of rodents (Krasnov et al., 2004); but most have reported no association, including helminths in mammals (Bordes et al., 2010; Poulin, 1995), helminths in primates (Nunn et al., 2005b), blood parasites in birds (Clark 2018) and ectoparasites of mammals (van der Mescht et al. 2018). When Kamiya et al. (2014) reviewed the determinants of parasite richness across plants, animals, and fungal taxa, no overall latitudinal effect was found, and where an association was found parasite richness was lower closer to the equator. This has been seen in other meta-analyses where increasing distance from the equator resulted in increasing parasite richness, for instance in protists in primates (Nunn et al., 2005), protists in rodents (Bordes et al., 2011), and trematodes in snails (Torchin et al., 2015). Altogether, these studies suggest that a latitudinal gradient in parasite species richness is worthy of investigation, but that unexpected patterns should be expected.

In this chapter, I aim to describe and explore patterns of variation in baboon gastrointestinal parasite communities through a meta-analysis of the available literature. I first ask if parasite community composition varies according to (Question 1, Q1) host specificity, (Q2) the phylogenetic distance between hosts, or (Q3) the geographic distance between populations. I then go on to ask whether environmental conditions influence (Q4) parasite community composition, as well as (Q5) the overall richness of the communities and (Q6) the presence/absence of the individual parasites that make up those communities.

METHODS

I compiled the published literature reporting the gastrointestinal parasite infections of baboon species using the methods previously described (see last chapter). The data were compiled from a total of 31 publications, with samples collected across five baboon species from 40 different study locations (Table 3.1, for a map of the study locations, see last chapter, Figure 3.1). For each study location, I recorded all the gastrointestinal parasites that were reported as present, together with their prevalence where available. Most studies presented data from overlapping troops as a single population (e.g. Benavides et al., 2012) but where overlapping troops were presented as separate data I combined these into a single data point

(two cases: Legesse & Erko, 2004; Müller-Graf et al., 1996). As some study sites had been repeatedly sampled, and to avoid pseudoreplication, each site was only represented by one randomly selected publication. Methods of sampling the parasites varied across studies. Many used the modified-formol ether concentration technique (Allen & Ridley 1970), or a variation thereof, to extract eggs and cysts from faeces. Others used alternative techniques to process faecal samples, or post-mortems, either alongside or instead of this concentration technique. However, data on the prevalence and abundance of most protozoa were too sparse for analysis, as many studies failed to report protozoa abundance or to identify protozoa to the species level. I did, however, analyse the environmental drivers of the prevalence of two protozoa species, *Balantidium coli* and *Giardia* sp., as these two were well reported. Thus the following analyses focus on helminth parasite communities (Q1-Q6) and these two protozoa species (Q6 only). All statistics were implemented in R environment version 3.3.3 (R Core team 2016).

Q1. Host specificity

To establish the similarity of helminth communities across baboon species, where the communities were defined according to both parasite presence and prevalence, I performed a non-metric multidimensional scaling (NMDS) analysis using the MetaMDS function from the vegan package (Oksanen et al., 2017). The NMDS analyses are non-parametric ordination plots and can include zero-inflated data, and for this reason are ideal for assessing the structure of parasite communities. I determined the most appropriate number of dimensions for the NMDS by determining goodness of fit through the Kruskal's stress value using the isoMDS function in the MASS package (Venables & Ripley, 2002). This showed that a three-dimensional analysis (k=3, stress=0.157) was most appropriate. I then assessed whether parasite communities are specific to baboon species (*P. cynocephalus*; *P. anubis*; *P. ursinus*; *P. papio;* and *P. hamadryas*) by looking for clustering in the similarity of the samples relative to the ordination distance between host species (Bray-Curtis), using 1,000 runs fitted using the envfit routine. I then used the adonis function to perform a permutational multivariate analysis of variance (PERMANOVA) using distance matrices to test for significant differences between clusters.

Table 3.1: Summary of research sites and publications used to compile the dataset.

Species	Site, Country	Mean temperature (°C)	Total rainfall (cm)	Seasonality Index (SI_i)	Mean NDVI	Reference
P. anubis	Aberdares, Kenya	16	85	0.444	0.676	[1]
P. anubis	Bugwe, Uganda	23	128	0.561	0.648	[6]
P. anubis	Bwindi, Uganda	18	144	0.440	0.747	[7]
P. anubis	Gashaka, Nigeria	24	151	0.675	0.706	[10]
P. anubis	Gilgil, Kenya	17	37	0.809	0.528	[12]
P. anubis	Gombe, Tanzania	20	114	0.627	0.640	[13] [14] [15]
P. anubis	Kibale Reserve, Uganda	23	94	0.448	0.786	[16] [17]
P. anubis	Kwano, Nigeria	24	151	0.675	0.706	[10]
P. anubis	Mau Narok, Kenya	13	108	0.547	0.499	[18] [19]
P. anubis	Mole, Ghana	28	120	0.666	0.464	[26]
P. anubis	Mpala, Kenya	17	77	0.425	0.449	[3]
P. anubis	Rift Valley, Ethiopia	16	101	0.476	0.257	[28]
P. anubis	Toro Reserve, Uganda	19	118	0.458	0.691	[2]
P. anubis	Yankari, Nigeria	27	91	1.022	0.448	[30]
P. cynocephalus	Amboseli, Kenya	22	73	0.862	0.317	[3] [1] [4]
P. cynocephalus	Kilifi, Kenya	26	100	0.618	0.251	[18] [19]
P. cynocephalus	Kimani, Kenya	21	76	0.947	0.369	[18] [19]
P. cynocephalus	Mahale Mountains, Tanzania	22	103	0.857	0.648	[24]
P. cynocephalus	Saadani, Tanzania	17	56	0.687	0.558	[31]
P. hamadryas	Al-Akhal, Saudi Arabia	27	14	1.102	0.075	[2]
P. hamadryas	Al-Baha, Saudi Arabia	21	1	1.066	0.167	[2]
P. hamadryas	Al-Rihat, Saudi Arabia	26	17	0.989	0.133	[2]
P. hamadryas	Al-Taif, Saudi Arabia	28	15	1.306	0.127	[2]
P. hamadryas	Asir Highlands, Saudi Arabia	29	17	0.643	0.195	[5]
P. hamadryas	Asir Lowlands, Saudi Arabia	30	14	0.915	0.172	[5]
P. hamadryas	Turabah, Saudi Arabia	23	24	1.122	0.102	[2]
P. papio	Fongoli, Senegal	29	128	1.067	0.497	[9]
P. papio	Mt. Assirik, Senegal	29	94	1.078	0.505	[27] [14]
P. ursinus	Cape Peninsula, South Africa	18	30	0.766	0.530	[8]
P. ursinus	Giant's Castle, South Africa	8	62	0.740	0.310	[11]
P. ursinus	Kruger, South Africa	23	67	0.784	0.343	[20]
P. ursinus	Kuiseb, Namibia	20	2	0.322	0.093	[21]
P. ursinus	Limpopo, South Africa	18	49	0.869	0.322	[22]
P. ursinus	Loskop, South Africa	19	67	0.805	0.397	[23]
P. ursinus	Mkuzi, South Africa	22	65	0.603	0.475	[25]
P. ursinus	Pringle Bay, South Africa	17	48	1.122	0.466	[8]
P. ursinus	Scrutton, South Africa	23	54	0.954	0.317	[23]
P. ursinus	Suikerbosrand, South Africa	16	60	0.852	0.356	[23]
P. ursinus	Tsaobis, Namibia	18	19	1.179	0.141	[29]
P. ursinus	Wildcliff, South Africa	17	57	0.392	0.418	[8]

Table 3.1: Summary of research sites and publications used to compile the dataset. Temperature and rainfall data were extracted for the first year that data were collected from the site, from the Willmott and Matsuura v4.01 climate data (Matsuura & Willmott, 2015). Publications used to compile the data: [1] Akinyi, 2017; [2] Ghandour, 1995; [3] Hahn et al., 2003; [4] Meade, 1984; [5] Nasher, 1988; [6] Ocaido et al., 2003; [7] Hope et al., 2004; [8] Ravasi et al., 2012; [9] Howells et al., 2011; [10] Weyher et al., 2006; [11] Appleton et al., 1986; [12] Eley et al., 1989; [13] Muller-Graf et al 1996; [14] McGrew et al., 1989; [15] Murray, 2000; [16] Freeland, 1979; [17] Bezjian et al., 2008; [18] Kuntz & Myers, 1967; [19] Myers & Kuntz 1968; [20] McConnell et al., 1974; [21] Appleton & Brain, 1995; [22] Goldsmid & Rogers, 1978; [23] Pettifer, 1984; [24] Kooriyama et al., 2012; [25] Appleton et al., 1991; [26] Ryan et al., 2012; [27] Ebbert et al., 2013; [28] Legesse & Erko, 2004; [29] Benavides et al., 2012; [30] Mafuyai et al., 2013; [31] Nonga et al. 2014.

Q2. Phylogeny

I then investigated whether similarity among helminth community assemblages was related to phylogenetic distance between the host species. Phylogeny was based on the five traditional *Papio* species (*Papio anubis*, *P. cynocephalus*, *P. hamadryas*, *P. papio* and *P. ursinus*), and the phylogenetic distances (established from mitochondrial DNA were provided by Newman et al. 2004). The similarity of parasite communities was derived through the Jaccard Similarity Index (β_j) (Jaccard, 1912):

$$\beta_j = a/(a + b + c)$$

where a is the number of parasite species found in both host species, b is the number of parasite species found in only the first baboon species, and c is the number of parasite species occurring only at the second baboon species. This is a common method for determining the similarity of parasite communities (Davies & Pedersen 2008; Poulin 2003; Koleff et al. 2003). The Jaccard Index was calculated using the vegan package (Oksanen, 2017) with the 'Jaccard' vare.dist function. The Jaccard Index is scaled between 0-1, with 0 showing no overlap in parasite communities, and 1 representing an exact match between two parasite communities. As the index is bounded between 0-1, I ran a Beta regression, using the Betareg package (Cribari-Neto & Zeileis, 2009), of β_j against the phylogenetic distance between baboon species.

Q3. Distance decay

To explore whether helminth communities differed across geographic space, I compared the Jaccard Index of similarity of two sites against the geographic distance between those sites. The Jaccard Index was calculated as described above. The geographic distances between the pairs of locations were calculated using the Geosphere package (Hijmans et al., 2019), using decimal latitude and longitude and accounting for the Earth's curvature. These data are not independent and were therefore analysed using a simple mantel correlation with 999 permutations, using the package ade4 (Dray & Dufour, 2007). I ran two mantel correlations, one across all baboon species, and the second excluding *P. hamadryas*.

Q4-Q6. Environmental drivers

I asked three questions involving environmental effects on baboon parasite communities. Here I describe how those variables were quantified before explaining each of the three

analyses in turn. Note that, due to the emergence of the *P. hamadryas* populations as outliers in the preceding analyses (see Results), the remaining analyses exclude this species.

Environmental variables

I considered seven different measures of environmental variability: latitude, altitude, annual rainfall, ambient temperature, climatic seasonality (indexed by rainfall seasonality), vegetation environmental productivity (using a satellite index), and provisioning. In many instances, the publications provided the latitude-longitude coordinates and the altitude of the site location, otherwise there was enough detail to determine this information from Google Earth (http://earth.google.com). Latitude was converted from distance North-to-South to distance from equator by converting negative latitudinal degrees into positive values. Monthly average temperature and annual rainfall data were taken from Willmott and Matsuura V4.01 (Matsuura, 2015). These data are derived from interpolation of land-based weather stations, which allowed access to data across the relevant time periods for all publications (1965 onwards). If faecal samples had been collected across multiple years, I extracted temperature and rainfall data for the first year of sampling. If no dates of sample collection were provided, I extracted data from the year previous to the publication date. Seasonality was determined from the distribution of rainfall events across the year, using the Seasonality Index (SI_i) (Walsh & Lawler, 1981):

$$SI_i = \frac{1}{R}\sum_{n=1}^{12}\left|X_n - \frac{R}{12}\right|$$

where R is the annual rainfall, and X_n is the total rainfall in month *n*. The index ranges from 0 to 1.83, moving from equally distributed rainfall across all months ($SI_i = 0$) to rainfall concentrated in a single month ($SI_i = 1.83$). Vegetation was determined through the 'greenness' of the habitat using remotely sensed data, i.e. the normalized difference vegetation index (NDVI) (Pettorelli et al., 2005). NDVI measures 'greenness' by deriving the difference between remotely sensed red and near-red wavelengths (Pettorelli, 2005). The NDVI for each study site was extracted from data provided through the Global Inventory Modeling and Mapping Studies (GIMMS), who produce the NDVI values from the National Oceanic and Atmospheric Administration's Advanced Very High Resolution Radiometer (NOAA-AVHRR). I used NOAA-AVHRR due to the availability of long-term data. As remotely sensed data were unavailable prior to 1982, any parasite data collected in previous years (n=11) to this were matched with NDVI data from 1982. Finally, the presence/absence of baboon feeding on human foods (provisioning) was assessed directly from the original paper.

Collinearity was tested between all seven variables using a Pearson correlation coefficients matrix. Where the correlation coefficient was above the standard |r|>0.7 threshold (Dormann et al., 2013) one of the correlated variables was removed from analysis (unless otherwise stated).

Q4. Testing environmental effects on parasite communities

To investigate if there were any environmental correlates of the helminth communities, I used the same NMDS analysis as described above (Q1), but with the additional fitting of explanatory variables. For this analysis, rainfall and NDVI were strongly correlated (|r| > 0.70), so NDVI was used to provide a reflection of the impact rainfall would have on the environment. The remaining environmental variables (latitude, altitude, temperature, seasonality, NDVI, and provisioning) were fitted to a three-dimensional NMDS (k=3, stress = 0.153), determining goodness of fit through the Kruskal's stress value. Ordination distances of parasite communities across baboon species were determined through Bray-Curtis using 1,000 runs. The environmental variables were fitted with envfit and statistical significance determined by the squared correlation coefficient (r^2).

Q5. Testing environmental effects on parasite richness

To explore the influence of baboon species and environmental variables on helminth richness I used a generalised linear model (GLM), using the 'glm' function in Rv3.3.3 (R Core team 2016). Richness was calculated as the total number of parasite species occurring at the study site, and was log-transformed to improve model fit. In this analysis, multicollinearity occurred between NDVI-rainfall (|r|=0.71) and latitude-baboon species (|r|=0.70). I therefore excluded rainfall and latitude. In addition, I included sampling effort as a predictor, determined by the number of samples collected at each study site, to control for the possibility that increased sampling could increase the likelihood of finding rarer parasite species. I also re-ran the models with latitude and rainfall in place of baboon species and NDVI, respectively. I used an information-theoretic approach for model selection (Burnham & Anderson, 2002), considering all possible combinations of fixed effects (including baboon species or latitude, NDVI or rainfall, temperature, seasonality, altitude, provision, sample effort) and compared the fit of each model through Akaike's information criterion adjusted for small sample size (AICc), with the R package MuMIn (Barton, 2016). AICc was used instead of AIC as the sample size is small in comparison to the number of estimated parameters (Burnham, 2002). All models within Δ6 AIC units of the model with the lowest AIC were selected. AIC often selects unnecessarily complex models, and when simpler versions of the

models with better AIC were also selected I retained these over the complex models ('the nesting rule': Richards 2008; Arnold 2010). If more than one model remained in the top set then model averaging was used to calculate the parameter estimates and standard errors of a final composite model. This final composite model was determined using the model.avg function in the MuMIn package with full-coefficient modelling. Any variables that had confidence intervals crossing zero were deemed to be an inconclusive result (du Prel et al., 2009).

Q6. Testing environmental effects on individual parasite species occurrence

To study the influence of baboon species and environmental variables on individual parasite species I used binomial GLMs. For each of four helminth species (*Trichuris* sp., *Oesophagostomum* sp., *Physaloptera* sp., and *Streptopharagus* sp.) and two microparasite species (*Balantidium* sp., and *Giardia* sp.) in turn, I assessed the environmental variables that were associated with their presence across populations. In the helminth analyses, similar patterns of multicollinearity were observed as above (Q5), and therefore the same approach was taken with the exclusion of variables and the re-running of analyses. In the protozoan analyses, the only multicollinearity was observed between latitude-rainfall ($|r|>0.70$); in these cases, I initially excluded rainfall and kept latitude, but then re- ran the models with rainfall in place of latitude. Once again, sample effort was also included in all models. All parasite species were assessed using binomial models with the logit link, except for *Giardia* sp. which used the cloglog link, using the 'glm' function in Rv3.3.3 (R Core team 2016). I used the same information-theoretic approach for model selection as described above (Q5).

RESULTS

Across 40 baboon populations, 16 protozoan parasite species and 32 helminth parasite species were reported. Although a substantial number of these parasites were widely distributed (eight protozoans and 12 helminths occur in >20% of populations), only a relatively small number were consistently found in the majority of communities (only four protozoans and three helminths occur in >50% of populations). This suggests considerable variation in parasite community composition across populations. I then went on to explore some of the potential sources of this variation, as described below.

Host specificity and phylogeny (Q1, Q2)

The helminth communities associated with each baboon species are illustrated in the NMDS ordination plot (Fig. 3.2). PERMANOVA confirms that four of the five baboon species exhibit very similar community patterns (F=0.69, df=1, r^2=0.02, p=0.7), with the only species with a distinct community being the hamadryas baboon (F=6.16, df=1, r^2=0.13, p=0.001). If *P. hamadryas* is removed from the analysis, the helminth communities of the remaining species show a high degree of overlap (Fig. 3.1). Nevertheless, the difference between *P. hamadryas* and the other baboon species did not appear to reflect phylogeny, since there was no significant relationship between the Jaccard Index of similarity and phylogenetic distance (Beta regression: Pseudo R^2=0.16, p=0.143).

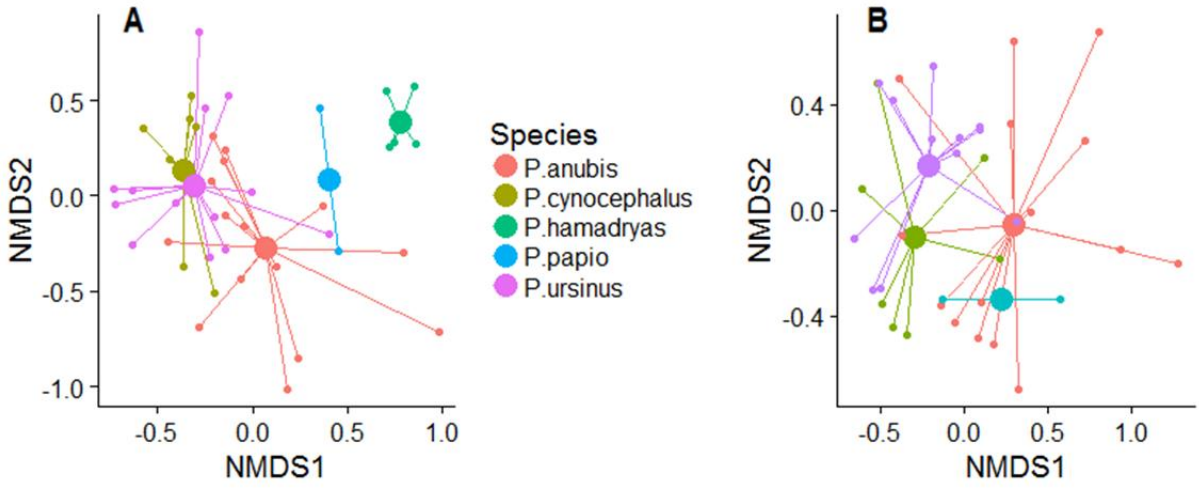
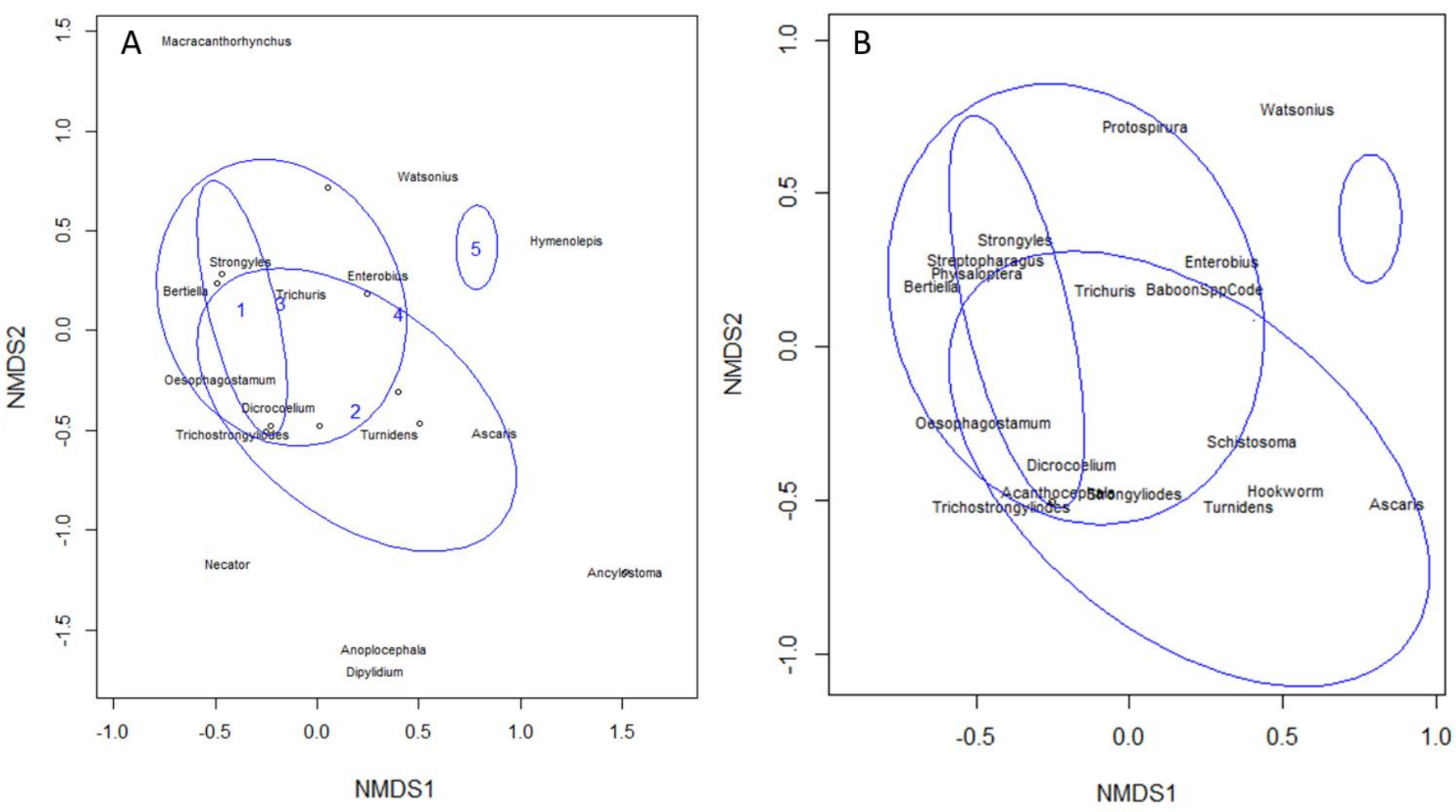


Figure 3.1: Two NMDS distance matrices of helminth communities to demonstrate the influence of *Papio hamadryas*, for (A) all baboon species, and (B) excluding *P. hamadryas*.

Figure 3.2: Plots of the ordinal distance of the helminth species, to illustrate the associations between different baboon and parasite taxa. **(A)** Plot to show the full spread of helminth taxa, with some central species names excluded for clarity (and instead represented by o). The baboon species positions are also indicated by the ellipses within the ordination plot: 1 = *P. cynocephalus*; 2 = *P. anubis*; 3 = *P. ursinus*; 4 = *P. papio*; 5 = *P. hamadryas*. **(B)** Plot to show the finer detail of the central helminth species.


A
Macracanthorhynchus
Watsonius
Hymenolepis
Strongyles
Enterobius
Bertiella
Trichuris
1
3
4
5
2
Oesophagostamum
Dicrocoelium
Trichostrongyliodes
Turnidens
Ascaris
Necator
Ancylostoma
Anoplocephala
Dipylidium
NMDS1
NMDS2
B
Watsonius
Protospirura
Strongyles
Streptopharagus
Physaloptera
Enterobius
Bertiella
Trichuris
BaboonSppCode
Oesophagostamum
Schistosoma
Dicrocoelium
Acanthocephala
Strongyliodes
Hookworm
Trichostrongyliodes
Turnidens
Ascaris
NMDS1
NMDS2

Distance decay (Q3)

Contrary to expectation, helminth communities did not become less similar with greater distance but more similar (Mantel correlation: *r*=0.34, p=0.001) (Figure 3.3). When I removed *P. hamadryas* from the analysis I still found a positive correlation (*r*=0.23, p=0.004) although with a reduced observable effect.

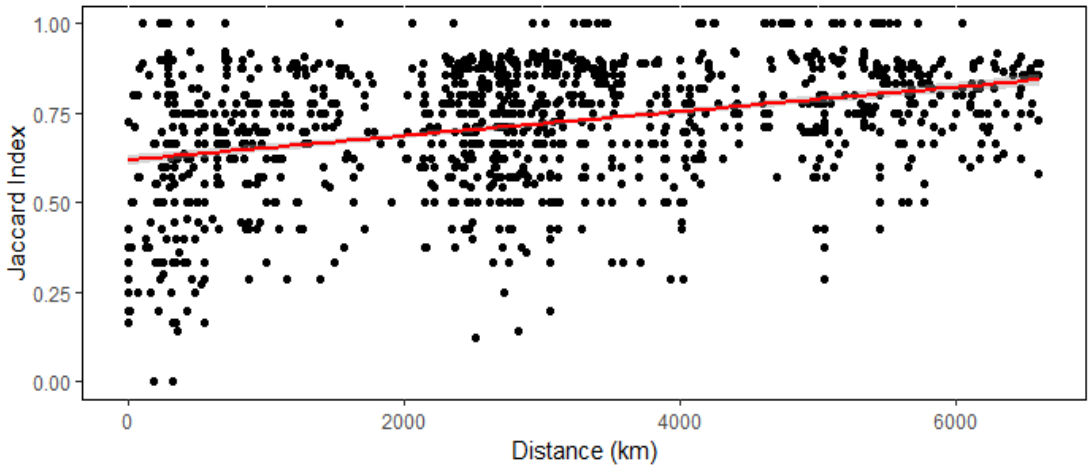


Figure 3.3. The relationship between the similarity of helminth communities and the distance between them.

Environmental effects on parasite communities (Q4)

Analysis of the environmental drivers of helminth parasite communities considered six potential factors: altitude, latitude, NDVI, temperature, seasonality and provisioning. Only one variable was found to be statistically significant, namely NDVI, although temperature also approached significance (Table 3.2, Figure 3.4). Including rainfall in place of NDVI showed it also was significantly associated with parasite community composition (NMDS: r^2=0.19, p=0.032). Populations with low NDVI/rainfall, such as Kuiseb River Canyon and Tsaobis Nature Park, had helminth communities characterised primarily by *Streptopharagus pigmentatus*. In contrast, populations with high NDVI/rainfall, such as Kibale National Park and Gombe National Park, were characterised by *Strongyloides* sp., and *Trichuris trichuria*.

Variable	r^2	p-value
Altitude	0.09	0.202
Latitude	0.05	0.401
Provision	0.01	0.891
NDVI	**0.31**	**0.003**
Temperature	0.14	0.097
Seasonality	0.05	0.404

Table 3.2. The six variables fitted as explanatory variables in the NMDS analysis of helminth communities, with r^2 and p-values.

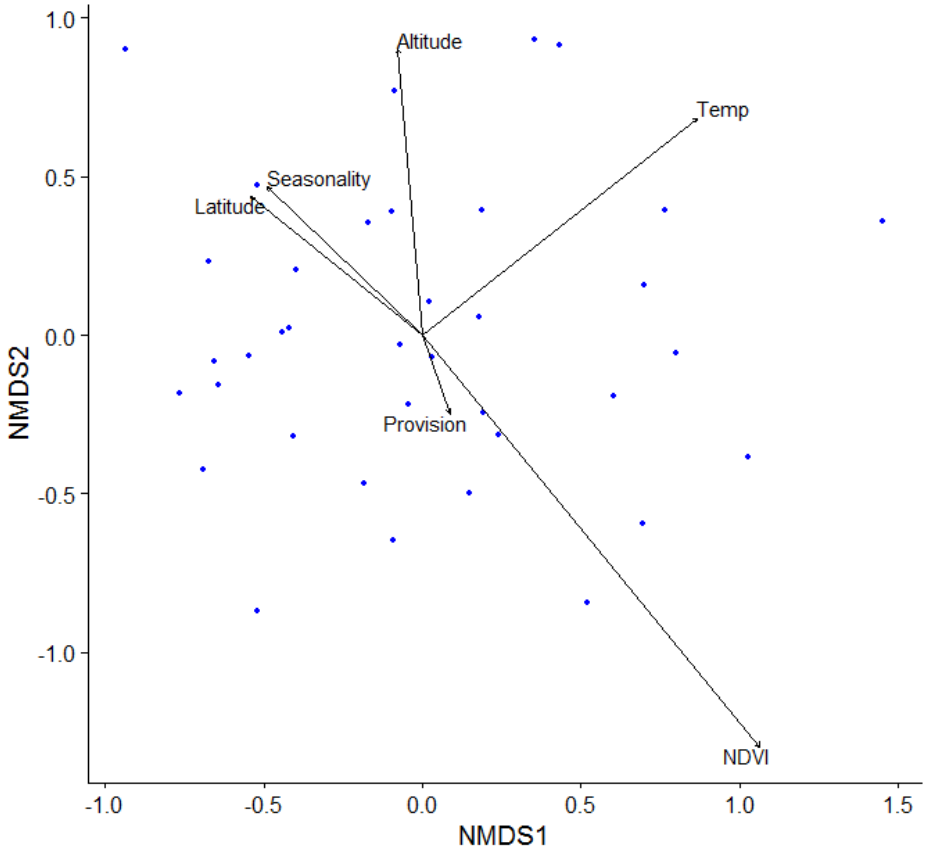


Figure 3.4. An ordination plot with the fitted environmental variables. The arrows show the direction of the gradient, and the length shows the strength of the correlation between the variable and the ordination. Only NDVI is statistically significant. Each point is one study site.

Environmental effects on parasite richness (Q5)

Helminth richness per population varied between 3-9 species, with a mean of 5.6 (mode of 6). Seven predictors of helminth richness were tested, comprising five environmental variables (altitude, NDVI, temperature, seasonality, and provisioning), plus sample effort and

baboon species as control variables. The final composite GLM (summarised in Appendix 1: Table S3.1) consisted of NDVI, temperature, and seasonality (Table 3.3, top row): richness was higher in more vegetated areas with greater seasonality and higher temperatures. However, the confidence intervals crossed zero in all cases so the importance of these variables is uncertain.

Table 3.3: The best composite and single GLMs identified through AICc model selection.

Analysis and species	Parameter	Estimate	Standard error	95% confidence intervals		Number of models
				Lower	Upper	
Helminth richness	NDVI	0.10	0.04	-0.03	0.18	4Ψ
	Seasonality	0.09	0.04	-0.05	0.16	
	Temperature	0.06	0.04	-0.04	0.05	
***Oesophagostomum* sp.**	Altitude	-2.68	1.86	-6.25	1.26	4Ψ
	NDVI	1.34	0.79	-1.06	2.28	
	Sample effort	-1.95	1.46	-4.39	1.57	
	Temperature	-2.43	1.55	-5.12	1.59	
***Streptopharagus* sp.**	NDVI	-1.00	0.49	-1.97	0.30	4Ψ
	Seasonality	0.71	0.46	-0.57	1.34	
	Rainfall	-0.03	0.01	-0.06	0.00	3
***Trichuris* sp.**	NDVI	0.68	0.45	-0.56	1.32	2Ψ
***Physaloptera* sp.**	Latitude	0.62	0.29	-0.32	1.15	3Ψ
	Rainfall*	-0.01	0.01	-0.01	0.01	
***Balantidium* sp.**	Latitude	2.84	1.59	-1.36	5.81	4
	Seasonality	1.08	0.66	-0.60	0.78	
	Altitude	-0.95	0.56	-0.64	0.50	
	NDVI	-0.98	0.64	-0.60	0.49	
	Rainfall*	-0.02	0.02	-0.02	0.02	5Ψ
***Giardia* sp.**	Latitude	-1.20	0.86	-2.48	1.02	2
	Seasonality	-4.30	2.58	-9.35	0.76	

Ψ Includes null model in the final model selection, * indicates the results of a second model run with rainfall instead of NDVI, and only indicates the results from the rainfall variable.

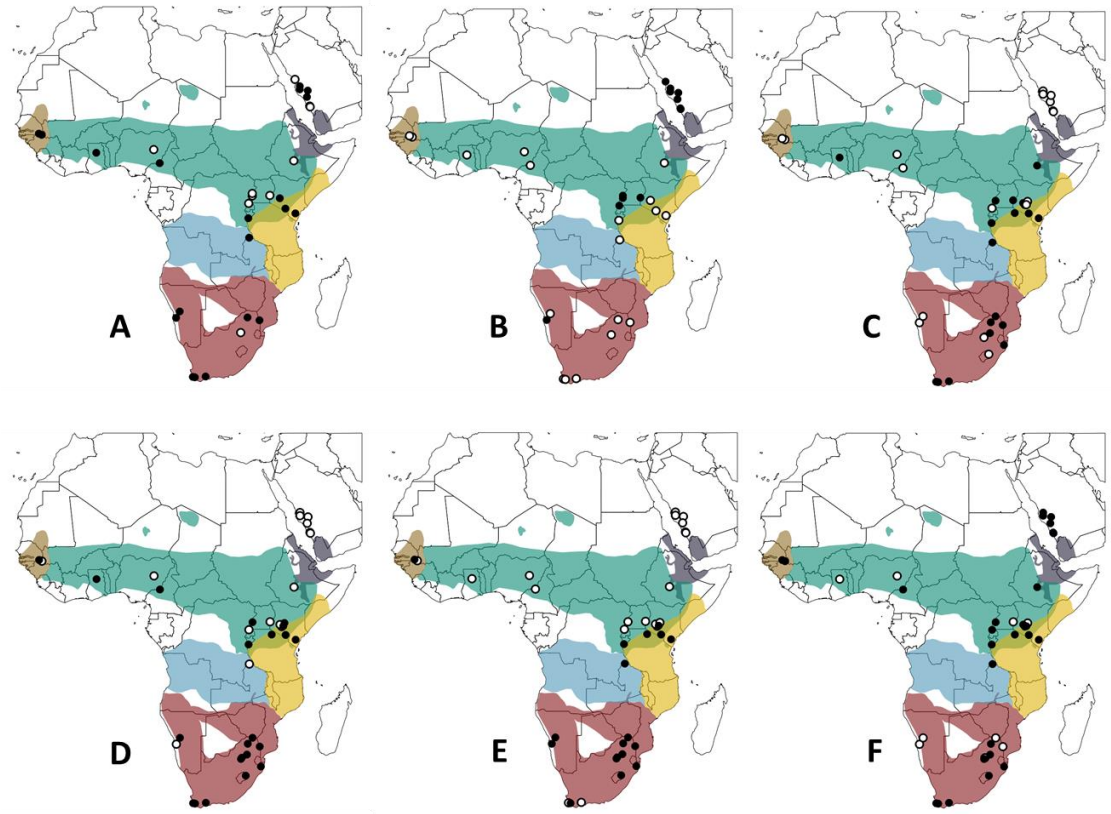


Figure 3.6: Distributions of six parasite taxa in relation to six baboon species: (A) *Balantidium* sp.*;* (B) *Giardia* sp.*;* (C) *Oesophagostomum* sp.: (D) *Physaloptera* sp.; (E) *Streptopharagus* sp.; (F) *Trichuris* sp. Parasite species presence/absence is indicated by the filled/open circles, respectively (taken from this study). Baboon species are plotted by colour*: P. papio* in brown, *P. anubis* green, *P. hamadryas* grey, *P. cynocephalus* yellow, *P. kindae* blue, *P. ursinus* red (taken from IUCN, 2017).

Environmental effects on individual parasite species occurrence (Q6)

The spatial distributions of the two most common protozoa (*Balantidium* sp. and *Giardia* sp.) and four helminths (*Oesophagostomum* sp., *Physaloptera* sp., *Streptopharagus* sp., and *Trichuris* sp.) across our study populations are summarised in Figure 3.6. Analysis of these patterns in relation to environmental variation revealed that NDVI and seasonality were the most consistent predictors across parasites (occurring in five and four models of the six best models, respectively, as illustrated in Appendix 1: Tables S3.2-3.5), although the direction of the effects differed between parasites (Table 3.3). In contrast, species identity did not enter any of the models. The remaining predictors appeared in 1-3 models. However, in all cases the confidence intervals crossed zero, so the results are inconclusive.

DISCUSSION

In this analysis I have described patterns of parasite community variation across baboon populations and explored some of the potential processes that might explain this variation. The results are summarised in Table 3.4. Here I discuss these findings in more detail.

Table 3.4. Summary of research questions, methods of analysis, and results.

Research question	Metric	Explanatory variables	Test	Results
Q1. To what extent are helminth communities similar across baboon host species?	Community composition (species presence/absence and prevalence)	Host species	NMDS PERMANOVA	No differences between species, with exception of *P. hamadryas* which differs from all others
Q2. Are patterns of helminth community similarity related to the phylogenetic distance between species?	Jaccard Index of similarity (species presence/absence only)	Phylogenetic distance	Beta regression	No effect of phylogenetic distance on similarity
Q3. Are patterns of helminth community similarity related to the geographic distance between populations?	Jaccard Index of similarity (species presence/absence only)	Geographic distance	Mantel correlation	Similarity is greater between more distant sites
Q4. Which environmental conditions are associated with particular helminth communities?	Community composition (species presence/absence and prevalence)	Latitude Altitude Annual rainfall Ambient temperature Climatic seasonality Environmental productivity Provisioning Sampling effort Baboon species	NMDS	NDVI/rainfall are predictors of community composition
Q5, Q6. Which environmental conditions are associated with helminth richness and individual protozoa and helminth species?	Number of species (richness) & Individual species (n=6) presence/absence	Latitude Altitude Annual rainfall Ambient temperature Climatic seasonality Environmental productivity Provisioning Sampling effort Baboon species	Gaussian GLM & Binomial GLM	NDVI, seasonality and temperature were predictors of species richness, but the effects were inconclusive & No conclusive effects are identified for any species, but the most consistent inconclusive effects are NDVI followed by seasonality.

Host specificity and phylogeny

I found that the gastrointestinal helminth communities are not distinct to each baboon species (*P. papio*; *P. ursinus*; *P. cynocephalus*; *P. anubis*) (Q1). The exception was the distinct community of parasites found within *P. hamadryas*, a species sampled only in Saudi Arabia, and therefore outside the African continent. This supports the findings of Gomez et al. (2013) where *Papio* species carry similar parasite species. The reason for the separation of *P. hamadryas* can be seen in Figure 3.1A, which illustrates which parasites are associated with each baboon species. Firstly, all the hamadryas baboon populations that were sampled (n = 6) are infected with *Hymenolepis* sp., a small tapeworm that is seen in only a few other African baboon populations: one Nigerian population (*P. anubis*: Mafuyai et al. 2013) and one Ugandan population (*P. anubis*: Hope et al. 2004). Secondly, and more importantly, are the parasites that are central on the NMDS and which feature across all the baboons species except *P. hamadryas*, including *Streptopharagus* sp., *Physaloptera* sp. (In Figure 1B), *Oesophagostomum* sp., *Bertilla* sp., and *Trichostrongyloides* sp. This pattern of hamadryas differentiation may reflect the fact that hamadryas baboons migrated into Arabia a long time ago. Based on the genetic divergence from African hamadryas populations, estimates of the timing of migration are between 37-74 kyr (Wildman et al. 2004) and 156-443 kyr (Winney et al. 2004). It may also reflect the different environment in which the Arabian baboons live. Although the Arabian Peninsula is grouped along with Sub-Saharan Africa in the same biogeographic region – the Afrotropical Realm – there are still likely to be important ecological differences between the two landmasses. Finally, it remains possible that all hamadryas baboons have a distinct helminth community from other baboon species. Although this seems unlikely, given the ecological similarity between all baboon species and the fact that I can rule out phylogeny as a possible driver (see Q2).Data from hamadryas baboons in Africa would be invaluable in allowing us to assess how such populations compare to other African baboon populations as well as the Arabian hamadryas baboons.

For parasite communities to be distinct within their host species, there must be some key biological differences (Poulin, 2000). Nunn et al. (2003) found that behaviour, particularly the use of landscapes, as the key component for species differences. As baboon species use their landscapes based on their home range ecology (Johnson et al., 2015) and baboon species do not each represent a distinct ecological niche (Winder, 2014), I would not expect to find species differences in movement behaviour or parasite community.

I found no association between the phylogenetic distance of baboon species and the similarity of their helminth communities (Q2). One possible explanation for this is that phylogeny is more likely to be an important factor when analysing parasite communities across phylogenetically distinct groups, and not within them (Dallas et al., 2019). Thus, baboon species may be too closely related to observe any signal in the divergence in their parasite communities. Alternatively, or in addition, Nunn et al. (2004) observed that whilst most parasite groups appear to diverge with their hosts, helminths are the exception, possibly due to their slower mutation rates. For these reasons, it is perhaps unsurprising that I did not see evidence of cospeciation between baboon species and their helminth parasites.

Distance decay

I analysed whether the helminth communities of baboons followed the expected pattern of distance decay, where the further away a host population the more dissimilar their parasites (Q3). Contrary to expectation, not only did the parasite communities not show a negative correlation with distance, they contradicted it entirely, with more distant populations harbouring more similar parasite communities. Poulin (2003) illustrates that distance decay is not universal across all host-parasite systems, possibly due to the features of parasite dispersal. Maybe I should not be surprised at this finding as many of the key parasites in baboon systems are able to infect multiple hosts, including primate species living in Asia (see previous chapter), and the scale of dispersal of these parasites appears to be large. A further complication is that there may be error in our assessment of community similarity due to our dependence on morphology for species identification. This really limits our ability to discern morphologically identical parasites, i.e. cryptic species, from each other. Indeed, many baboon parasites are almost ubiquitous across the continent, raising the question of whether there are actually multiple species currently being treated as a single species. Nevertheless, while these arguments may help to explain the lack of a negative correlation, they are less effective at explaining a positive correlation. One possibility is that this correlation arises because the distribution of baboon populations in this study straddles the equator, and there is a tendency for more distant sites to occur in more similar environments because they occupy similar latitudes above and below the equator. Such an explanation requires further investigation, but is consistent with the observation that, in other studies of parasites where the environmental similarity and the spatial proximity have both been considered, environment was the main predictor of parasite community similarity (Krasnov et al., 2010; Qian & Ricklefs, 2012). I go on to discuss my findings in relation to environmental effects on the parasite communities of baboons below.

Environmental effects

The most important environmental effect on baboon parasites appeared to be NDVI and/or rainfall, the two effects could not be distinguished. This pattern was consistent across three sets of analyses. First, NDVI/rainfall was associated with the composition of helminth communities, with wetter, more vegetated habitats characterised by different helminth species than dryer, less vegetated, habitats (Q4). Second, helminth species richness was higher in wetter, more vegetated areas, although this result was inconclusive due to the wide confidence intervals (Q5). Third, the occurrence of three of four helminth species (*Oesophagostomum* sp., *Streptopharagus* sp., *Trichuris* sp., not *Physaloptera* sp.) and one of two protozoan species (*Balantidium* sp., not *Giardia* sp.) was associated with wetter/more vegetated or dryer/less vegetated conditions, although again these results were inconclusive (Q6). These patterns are consistent with the idea that individual parasite species, and the communities which they create, are sensitive to local environmental conditions. However, the precise mechanism through which NDVI/rainfall affects baboon parasites remains unclear: both environmental predictors are likely to be associated with the availability of surface water, microhabitat climate (especially shade and moisture), host foraging habits and ranging patterns, and the abundance and behaviour of intermediate invertebrate vectors. All these factors could play a role in the transmission of parasites between hosts, either alone or in combination.

CHAPTER FOUR

Methods

STUDY SYSTEM AND GENERAL METHODS

The study system used to explore the population- and individual-level factors associated with baboon gastrointestinal infections was a desert-dwelling population of wild chacma baboons (*Papio ursinus*). This study population is part of the Zoological Society of London's long-term Tsaobis Baboon Project, based at Tsaobis Nature Park, Namibia (22°23'S, 15°45'E). In this Chapter, I will provide a description of the study system, the collection of data and samples in the field, and their subsequent analysis. I will also explain how I quantified environmental variation at the landscape scale.

STUDY SYSTEM

Study species

Chacma baboons range throughout southern Africa, living in multimale-multifemale groups: troops. These troops are generally composed of 20-80 individuals. Females remain in their natal group throughout their life, whereas when males reach sexual maturity – which occurs around 8 years old – they disperse to another troop (Bergman et al., 2003; Bulger, 1993; Seyfarth, 1976). Baboons are not seasonal breeders and so infants are conceived and born all year round (Alberts et al., 2005; Cheney et al., 2004). Chacma baboons are polygynandrous; however, male access to mating opportunities is dependent on dominance rank, and as a result the dominant males monopolise breeding opportunities (Bulger, 1993; Weingrill et al., 2003). Dominance hierarchies are linear across both sexes: females inherit their rank from their mother, forming matrilines (Bergman, 2003; Seyfarth, 1976; Silk et al., 1999); juvenile males inherit their rank from their mother, but increases with age (Cheney & Seyfarth, 1977; Johnson, 1987; Lee & Oliver, 1979); and adult males establish their dominance through challenging their rivals (Bulger, 1993; Kitchen et al., 2005). Males are nearly twice the size of females, and so all adult males rank above all adult females.

Study site

The baboons in this study range across a private nature reserve, Tsaobis Nature Park, and two neighbouring farms. This area of land, hereafter 'Tsaobis', is situated in the Erongo region

of Central Namibia (Fig. 4.1). The region is semi-arid with low and highly seasonal rainfall. The mean annual rainfall is 122mm (n=68 years) falling in the austral summer (October – April). In the shade, temperatures usually range between 13.5°C - 31.6 °C (mean daily minimum and mean daily maximum across field seasons, 2002-2017), with a range of 0.6 °C – 46.0 °C.

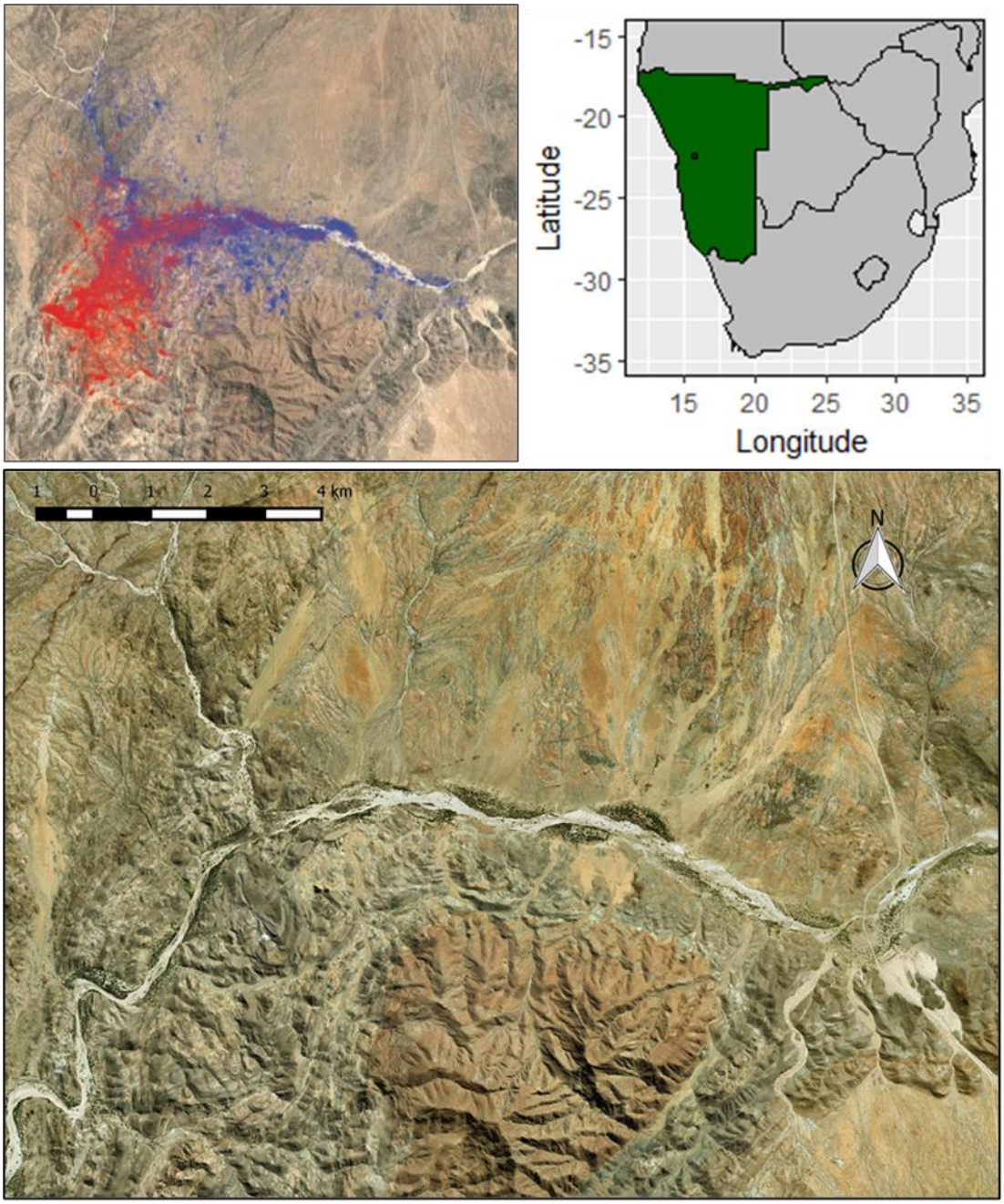


Figure. 4.1. Top right panel: Map of southern Africa, with Namibia highlighted in green, and the study site shown in the rectangle. Main panel: Satellite photo of the Tsaobis study site where the two baboon study troops range. This is cropped to the furthest Northern, Southern, Easterly, and Western GPS locations of the two baboon study troops recorded from all the study years (2005 onwards). Top left panel: The same image with GPS points plotted for the two troops, with J troop in red and L troop in blue.

The altitudinal range of Tsaobis is between 683 – 1445 m. Bisecting the study site is an ephemeral river, the Swakop, which remains dry for most of the year but occasionally has flowing water during some rainy months. Despite the fact it is dry, the riverbed supports much of the large trees and bushes, thanks to a high watertable persisting subsurface year-round. The vegetation is predominated by the trees *Faidherbia albida* and *Prosopis glandulosa*, and the shrub *Salvadora persica*. The Swakop's tributaries are similar in habitat, especially the Gaumikaub which feeds into the Swakop from the North (Fig. 4.2). Moving away from the river brings alluvial plains or steep-sided hills and mountains. Here the habitat is more open, dominated by grasses, small herbs, shrubs, and small trees, for example: *Monechma cleomoides*, *Sesamum capense*, and *Commiphora virgata*. Further details about the vegetation of Tsaobis can be found in Cowlishaw & Davies (1997).

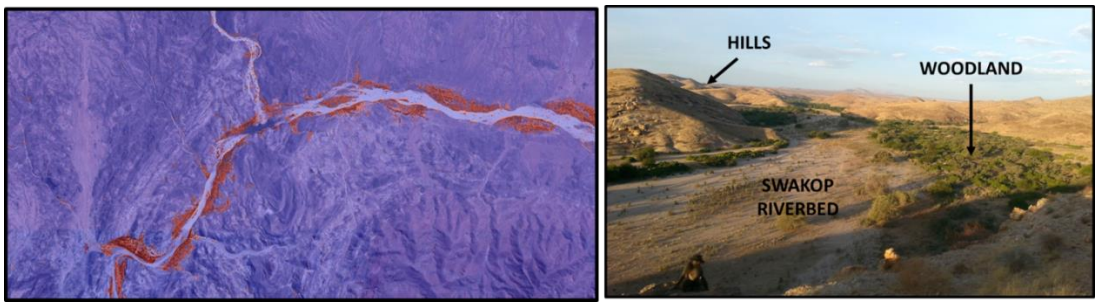


Figure 4.2. Left hand panel: Satellite photo of Tsaobis, with the locations of trees coloured in red, highlighting the fact that they are distributed along the Swakop river, and some way up the Gaumikaub river. Right hand panel: Photo of the Tsaobis landscape showing the woodland along the Swakop, the dry riverbed, and the hills around the riverbed.

Study populations

The baboons

The Tsaobis Baboon Project was set up with an initial study of the baboons in 1990 (Cowlishaw, 1997). Since 2000 the project has been conducting yearly field seasons, usually centred around the austral winter months (April – November), to monitor the ecology, demography, and behaviour of these baboons. Since 2005, the project has focused on two study troops, troop L and troop J, which contained 57 and 61 individuals respectively during my 2014-2015 field season. These troops have minimal contact with people other than the research team. All individuals are habituated to the presence of human observers following at close proximity (Fig. 4.3A). Ranging and foraging behaviour and individual interactions

occur entirely naturally, unless the research team are conducting field experiments or troop captures, which occur across only a few weeks in occasional field seasons.

All baboons are individually identifiable using ear notches or other distinguishing features (Fig. 4.3B). Ear notch combinations are unique to each individual baboon and are created by a veterinarian whilst the baboons are under anaesthetic during whole-troop capture events. The process of making the ear notches allows for a small tissue sample to be collected for genetic analysis. In addition, during capture the baboons are weighed and measures of morphology taken, such as crown-rump length and skinfold thicknesses, to assess body condition.

Figure 4.3. (A) Data collection occurs in close proximity but at an appropriate distance so as not to disturb normal behaviour; (B) Ear notches, in this case on the middle and bottom of the ear, help to identify the individual.

The baboon troops begin their day at their sleeping cliff. Shortly after dawn, the baboons descend from the cliff and begin to forage, either foraging across the desert hills and plains if there are still food plants and insects available after the summer rains, or travelling directly to forage in the Swakop Riverbed if the desert vegetation has died back following the rains. In between foraging bouts, the baboons stop to rest and socially interact with one another through grooming. The baboons also normally drink once a day by visiting a waterhole. Eventually, as evening approaches, the baboons travel to a sleeping cliff for the night. See Fig. 4.4.

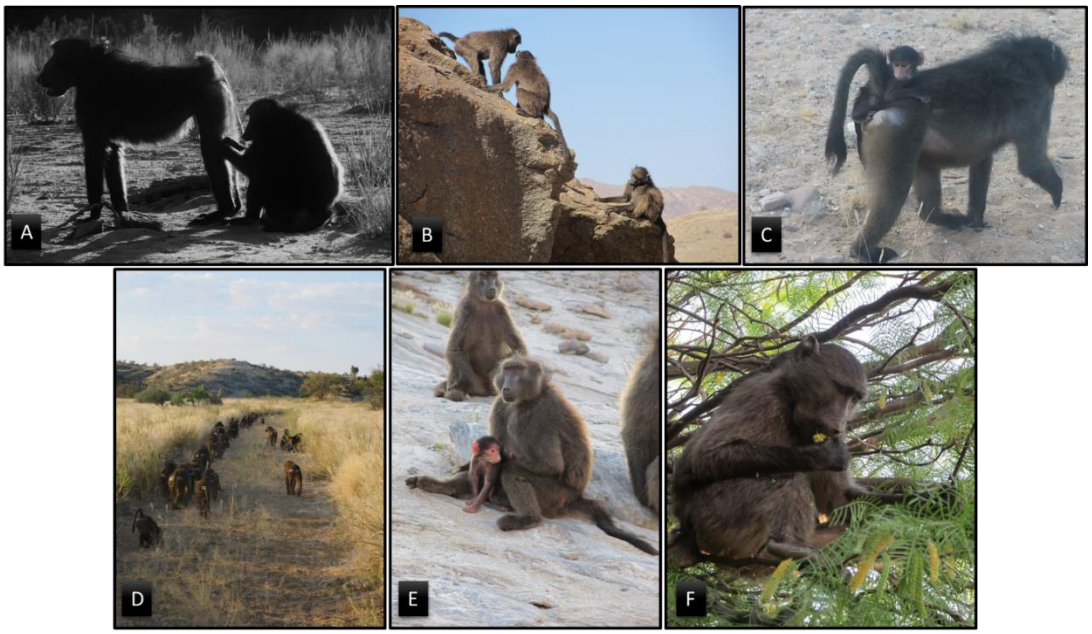


Figure 4.4. Photos of the Tsaobis chacma baboons. (A) Adult male Plato being groomed by adult female Yaounde; (B) Juveniles playing; (C) Adult male carries infant on back: (D) L troop travelling across the plains; (E) Adult female with her infant; (F) Juvenile eating *P. glandulosa* flowers.

Identification of males and females, and the monitoring of female reproductive states, is straightforward. Males are nearly twice as large as females in adulthood, and from birth have continuous ischial callosities rather than separate pads (see Fig. 4.5). Females cycle all year round, unless pregnant or lactating. As ovulation approaches, they develop sexual swellings which reach maximal size at ovulation (Fig. 4.5B). Pregnancy is also indicated by a reddening of the paracollosal skin (Fig. 4.5C).

Figure 4.5. Establishing sex and reproductive state. Lefthand panel: Male ischial callosities are continuous unlike those of females which are two separate pads (seen in Centre and Righthand panels). Centre panel: Female with reproductive swelling which develops during oestrus and is largest at ovulation. Righthand panel: Female with red paracallosal skin around the ischial callosities, indicating pregnancy.

The parasites

The Tsaobis baboons harbour a range of microparasite species and a relatively small number of macroparasite species (Benavides et al. 2012a). Among the macroparasites, the two main nematode species are *Streptopharagus pigmentatus* (Fig. 4.6A) and *Physaloptera caucasia* (Fig. 4.6B). Both are indirectly transmitted. It is assumed at Tsaobis that they are transmitted via desert locusts (*Schistocerca gregaria*) and other small Orthopteran species on which the baboons forage. Other nematodes observed in this population, such as *Ascaris* sp., *Subulura* sp., and *Macracanthorhynchus hirudinaceus*, are rare: they had a prevalence ≤0.02% in 2005-6 (Benavides et al. 2012a) and have not been observed since. There has also been evidence of *Toxocara* sp. (Fig. 4.6C), although again at a low prevalence (0.2%) across all years (2005-2015). The microparasites include one ciliated protozoan species, *Balantidium coli* (Fig. 4.6D). Additionally, there are multiple amoeba species: *Entamoeba* spp. (Fig. 4.6E), *Chilomastix mesnili*, *Dientamoeba fragilis*, and *Iodamoeba buetchlii*. All these microparasites are directly transmitted either through host-to-host contact or faecal-oral routes via the environment. Further information about the prevalence of these parasites at Tsaobis is presented later in this chapter. Further information about the biology of these parasites and their pathogenicity was reviewed in Chapter 2.

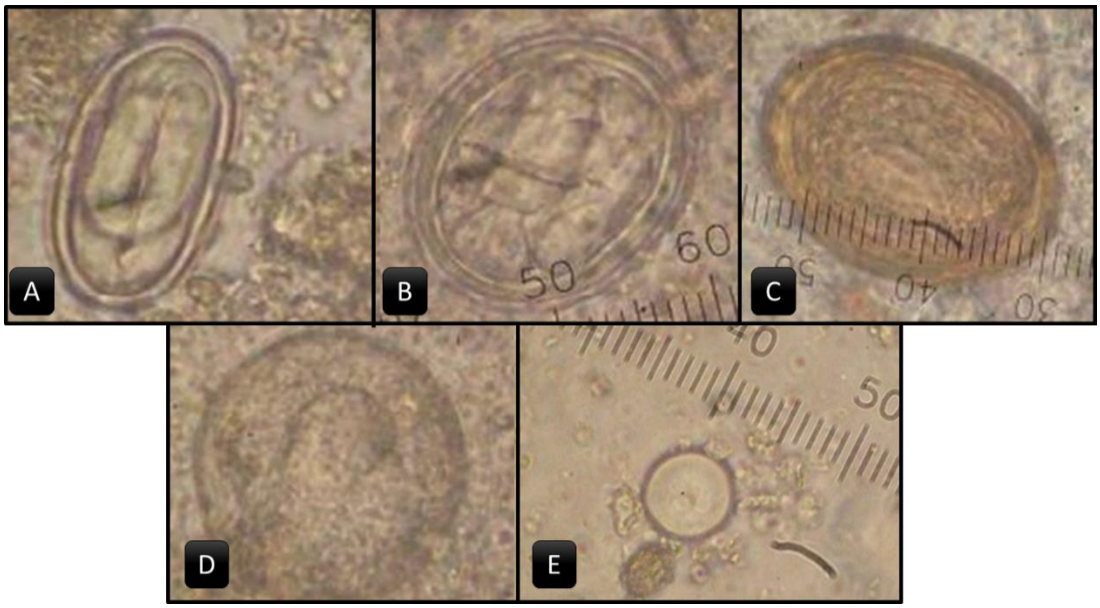


Figure 4.6. Photos of some the parasite eggs and cysts seen in the Tsaobis baboon faecal samples (Note: sizes are not comparable). (A) *Streptopharagus pigmentatus*; (B) *Physaloptera caucasia*; (C) *Toxocara* sp.; (D) *Balantidium coli*; (E) *Entamoeba* sp.

DATA AND SAMPLE COLLECTION

The data analysed in this thesis are based on field observations and samples collected from the Tsaobis baboons in 2005-2006 and 2009-2015. Although my PhD fieldwork was only conducted in 2014-2015, I also participated as a volunteer field assistant and contributed to the data and sample collection throughout two prior field seasons, in 2011 and 2012. In addition, I have taken primary responsibility for the laboratory analysis of the faecal samples to analyse parasite infections since 2009, either carrying out the analysis myself or acting as the supervisor and trainer of the MSc students or student volunteers who carried out the work. A summary of the key field data used in this study is provided in Table 4.1.

Data	Method	Total years	Years I contributed	Chapters
Parasites in baboon faeces	Faecal samples, Microscopy	2005-06, 2009-15	2011-12, 2014-15	5,6,7
Defecation location	GPS points	2014-2015	2014-15	5
Home range, Area use	GPS points	2005-2015	2011-12, 2014-15	5
Dominance hierarchy	Ad lib, focals, MatMan	2005-2015	2011-12, 2014-15	6
Social network	Ad lib, and focal	2009-2015	2011-12, 2014-15	6
Individual state (age, sex)	Demography data	2005-2015	2011-12, 2014-15	5,6,7
Inbreeding, msat and MHC genotyping	Tissue samples, sequencing	2005-06	None	7
Microhabitat temperature	Thermologgers	2014-2015	2014-2015	5
Parasites in the environment	Soil and water samples, microscopy	2014-2015	2014-2015	Appendix 5

Table 4.1. Summary of the field data and samples collected, the years for which these data and samples are available and the years I contributed, and the chapters of this thesis in which these data and samples are used.

Behavioural data collection

The fieldwork I carried out in 2011 and 2012 involved a 2-month field season and a 6-month field season, the latter including whole-troop capture events for both L and J troops. For my

PhD I then planned a 12-month field season from July 2014-June 2015, to collect data across a full annual cycle, but unfortunately due to a head injury I sustained during a car accident my field season came to a premature end after six months in Jan 2015. Broadly speaking, my data collection protocols in 2014-2015 were similar to those used at Tsaobis in previous years, unless otherwise stated below. However, I was fortunate that the data collection that was unique to my PhD project were continued on my behalf by the field team during the following 6-month field season at Tsaobis, between Apr – Sept 2015.

Daily data collection from the baboons involves following the troops on foot, with two team members working together on each troop, from dawn until dusk. Full-day follows are necessary because the baboons typically walk 6 km per day (Benavides et al. 2012a) and where they will finish the day (and hence begin the next day) is very difficult to predict from where they started that day given the choice of many sleeping cliffs (n = 117). We arrive at these cliffs each morning before sunrise, and remain with the troop until they reach their next sleeping cliff at sunset, following the troops from approx. 5am until 7pm.

My PhD field season in 2014-2015 was planned to be the first field season to cover a full annual cycle. All previous field seasons have tended to focus on the austral winter (April to November), when the days are shorter and less extreme in temperature, although still hot. This deviation from the normal field season meant that we were exposed to unusually difficult working conditions with longer days and higher temperatures. To mitigate this, we began following each troop for half a day before switching team members who were rested. Due to the limited size of the field team, this meant that we alternated which of the two troops we followed. Initially I co-ran the field season with another PhD student, Alice Baniel, from July-Nov 2014, where we shared 4-8 volunteers. I then ran the field season from Nov 2014 - Jan 2015 with a team of 7-9 volunteers.

Troop movement data

Movement data were collected daily to record the route that the baboon troops travelled throughout the day. The recording started at the sleeping cliff using a handheld GPS (global positioning system) device and continued to be marked with a waypoint every half hour. These points were recorded until the baboons ascended onto their sleeping cliff for the night. In addition to these points, a higher resolution route was also produced through constant

recording of the GPS track as we walked with the troop. However, only the former data are available for all previous years, so for this study I only use the half hourly GPS points.

Individual behavioural observations

Behavioural observations were collected in line with Altmann (1974) protocol, utilising three techniques: focal follows (hereafter 'focals') and *ad libitum* recording at the individual level, and instantaneous scans at the troop level.

Focals involved following an individual for 30 minutes and recording all of the individual's interactions (affiliative and aggressive) including the identities of all partners in those interactions, and activities (such as feeding, travelling, resting, and grooming) including their durations. Other data collected included the foods eaten, habitats used, spatial position within the troop, and self-directed behaviours (such as scratching and self-grooming). Data were also collected on spatial associations with other group members using three complementary approaches: the nearest neighbour within 5m, all baboons within a 10m radius, and all individuals linked within 5m of each other. The first measure was collected continuously during the focal, whereas the second and third measures were both collected at the beginning and end of the focal. During my 2014-2015 field season, I focussed on a subsample of 46 baboons, 23 individuals from each troop, who were carefully selected to represent a full range of individual age, sex, and rank classes. In total my field team and I conducted >400 30-min focals per troop. These focals were spread across four months of main data collection (Oct 2014 – Jan 2015). Focals were distributed across four time zones in the day (0600-0900, 0900-1200, 1200-1500, 1500-1800), such that for each month the focals were evenly spread across the four time periods for each individual.

Ad libitum data collection involves observing social interactions opportunistically, and is especially helpful in recording (1) the winners and losers in aggressive interactions, to ascertain an individual's position in the dominance hierarchy, and (2) the frequency different individuals spend grooming others, to ascertain social relationships and the emergent social networks.

Instantaneous scan data provides a troop-level approach to data collection. Every half hour, when a GPS point is taken, a troop scan is also made and the activities of all visible baboons, the area of troop spread, and the habitat occupied, were recorded.

For 2014-2015, these data were collected using Cybertracker (http://cybertracker.org), which allowed me to build a user-friendly interface (Fig. 4.7) that time-stamps the events.

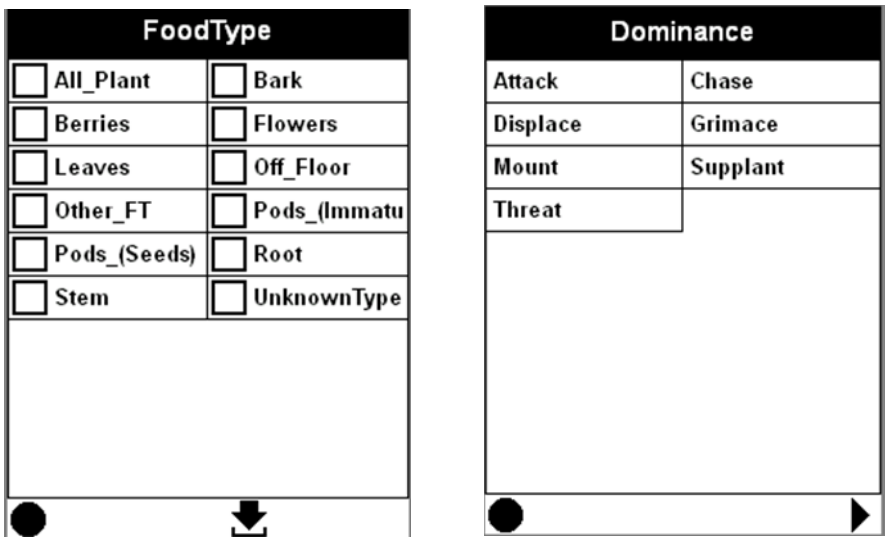


Figure 4.7. Example screens in the Cybertracker software for focal data collection used in this study.

Ecological data collection

A variety of ecological monitoring data were collected in parallel with the behavioural data collection. The two key datasets that I collected in my 2014-2015 field season that I use in this study were as follows.

First, soil and water temperature. Thermologgers (ETI thermometers) were placed in various locations under the soil surface or within water sources to continuously monitor hourly variation in temperature across days and months. These data were collected to understand the range of temperatures that the baboon parasite cysts and eggs might be exposed to, and therefore their ability to remain viable, under different conditions during the year. These data are described in further detail where they are used in Chapter 5.

Second, soil and water sample collection. Samples of soil and water from locations around the study site were collected each month and stored in 10% formalin. These data were collected to assess which areas of the environment might contain the greatest density of parasite cysts and eggs, and therefore pose the greatest risk in terms of parasite exposure and subsequent infection. These data are described in further detail in Appendix 5.

Faecal sample collection

Faecal samples for parasitological analysis were collected from my subsample of 46 baboons on a monthly basis. These samples were taken every fortnight by observers throughout the day and stored in 10% formalin within 5 minutes of defecation. In 2014-2015, when collecting a sample, a GPS point was also recorded, along with details of the morphology of the faeces. The recommended size of the faecal pellet taken was 0.5g; any with a weight less than 0.04g were excluded from the analysis. During the 2014-2015 field season, we collected 916 samples.

DATA AND SAMPLE ANALYSIS

Below I describe how the key individual attributes of age and dominance rank were calculated, and how the faecal samples were analysed for parasites. The description of how other individual attributes were calculated, such as social network position, are provided in the relevant chapters. The methods of statistical analysis are similarly described in the relevant chapters.

Quantifying individual baboon attributes

Age

The age of a baboon born into a troop during a field season can be calculated from its observed date of birth. To estimate the ages of those baboons whose birth we did not witness (i.e. born before the study began, immigrated into the troop, or were otherwise born between field seasons) we used dental examination involving a combination of tooth eruption and molar wear (Huchard et al., 2009). The method has been validated by using individuals captured on multiple occasions (n = 19 over 1-5 years) to compare known age differences against the estimated age differences, which show no statistically significant differences (one-sample t-test, $p>0.05$; G. Cowlishaw, unpublished data). These examinations occurred during whole-troop capture events whilst the baboons were under anaesthetic.

Dominance rank

The dominance ranks of individuals were established for each field season using data on aggressive interactions from both focal observations and *ad libitum* observations. These data record the wins and losses in dyadic approach-avoid interactions (supplants and displacement behaviours) and agnostic interactions (attack, chase, and threat behaviours) between all identifiable individuals (see Huchard & Cowlishaw 2011 for definitions). If one individual could not be identified then the interaction was not included in the analysis, and if more than one dominance behaviour was exhibited within one event, only one interaction was recorded. These dyadic interactions were used to build a dominance hierarchy, and thus assign individual dominance ranks, using Matman 1.1.4 (Noldus Information Technology, 2013). Dominance rank was expressed relatively to control for group size and thus make positions comparable across years, using the formula 1-[(1-r)/(1-n)], where r is the absolute rank and n is the group size. Individual relative ranks range from between 0 (lowest rank) to 1 (highest rank).

Analysing faecal samples for parasites

The faecal samples were processed using the modified formol-ether concentration technique, as described by Allen & Ridley (1970). This method is the most commonly used technique implemented in baboon parasite studies (See Chapter 2). In 2005-2006, the samples were processed in a specialist parasitological laboratory in South Africa (Benavides et al. 2012a). Since 2009, the samples have been processed in the UK at the Institute of Zoology, in consultation with, and taking care to follow the same protocols as those used in South Africa.

The modified formol-ether concentration technique allows the calculation of the abundance of eggs and cysts of different parasite species expelled in the faeces of an individual. Using light microscopy, every nematode egg is identified and counted. The protozoa and are given a score of infection intensity, so that cysts per gram are categorised (0-6) (to avoid counting the large numbers present). To determine parasite richness, the number of different parasite species per host was counted (see Margolis et al 1982). However, the identification of the amoeba species (i.e. all protozoa except *Balantidium coli*) by morphology alone is difficult using microscopy, with some species sharing an identical appearance (e.g. *Entamoeba dispar* and *Entamoeba histolytica*). For this reason, the amoebae were grouped into two categories, referred to as 'Medium amoeba' and 'Small amoeba'. The medium-sized amoeba category

corresponds to the grouping of *Entamoeba chattoni*, *E. histolytica, E. dispar, E. coli, and I. buetchlii*. The small-sized amoeba category includes *E. hartmanni, E. nana,* and *D. fragilis*.

Of the samples returning for the 2014-2015 field seasons, 350 were processed in this way. Across all years, a dataset of 1,888 processed faecal samples have been produced. The breakdown of samples across years is described in Table 4.2. In total 163 individual baboons were included in the dataset, sampled between 1-59 times (mean = 11; mode = 2), with 820 males sampled and 1073 females sampled. The age of individuals ranged between 28 days old to 24.9 years old. Of these samples, 13 were below the 0.04g threshold for inclusion into the analyses, and 11 individuals were not included as their age was unknown. Therefore, a total of 60 samples were excluded.

Year	**Number of samples**	**My contribution (C=collected, A=analysed, S=supervised analysis)**
2005	340	-
2006	352	-
2009	281	A
2010	157	A,S
2011	108	C,A,S
2012	182	C,A,S
2013	121	A,S
2014	137	C,A,S
2015	210	C,A,S

Table 4.2. Summary of the number of faecal samples each year processed and analysed in order to contribute to the dataset used in this thesis, together with my involvement in the collection, analysis, and the supervision of the analysis of those samples.

The overall pattern of prevalence for the different species and species categories across this full sample is summarised in Table 4.3.

Species	Median	Range	Prevalence	Parasite phylum
Streptopharagus pigmentatus	11.7	0 - 5,154	81%	Nematode
Medium-sized amoeba	2.0	0 - 6	84%	Amoeboid
Balantidium coli	1.0	0 - 4	81%	Ciliate
Small-sized amoeba	0.0	0 - 6	45%	Amoeboid
Physaloptera caucasia	0.0	0 - 76	15%	Nematode
Chilomastix mesnili	0.0	0 - 5	11%	Flagellate

Table 4.3. Summary of the parasite data from all years (2005-2006, 2009-2015). Medium-sized amoeba category corresponds to the grouping of *Entamoeba chattoni*; *E. histolytica*; *E. dispar*; *E. coli; I. buetchlii*. The small-sized amoeba includes *E. hartmanni*; *E. nana*; *D. fragilis*. For protozoans the median, range, prevalence, refers to the score rather than the absolute values.

Limitations of methods for quantifying infectious status

When studying the health status of wild animals often non-invasive sampling is the most viable method. The low cost of coproscopical methods have further supported the ability to assess health of multiple individuals over long time periods through repeated sampling. For these reason faecal samples have become a popular method of health monitoring and disease ecology research, and has resulted in much of the parasite research to have focused on gastrointestinal parasites. The method used in this thesis for extracting parasites eggs/cysts from the faecal samples (the modified formol-ether concentration technique: Allen & Ridley, 1970) is the most commonly used technique implemented in baboon parasite articles (see *Chapter three*). Using techniques across study sites creates a dataset where we can directly compare parasite communities across the host populations, creating the opportunity for a broader scope of research (Gillespie, 2006). Additionally, as with all long-term projects, keeping the methodology consistent across all our years of study has provided the opportunity to include all data into the analyses. Faecal samples were previously collected in 2005 and 2006, and processed in South Africa using the modified formol-ether concentration technique (Allen, 1970; Benavides, 2012a), and since 2009 we have been following the same protocol.

It should be acknowledged, however, that all methods for non-invasive and non-destructive sampling of parasites have limitations in their reliability, repeatability, and accuracy. Interestingly, there are some concerns about the viability of using the modified formol-ether for primate faecal samples. This method separates the faecal material from the eggs, leaving

the eggs to at the bottom of the sample, and the remaining material held between the layers of the two immiscible liquids: ether and formaldehyde. According to MAFF (1979) this method is most effective in faeces from animals with high fat diets, for example domestic and carnivorous animals. Baboons, whilst omnivorous, generally have a folivorous diet, and for this reason Howells et al. (2011) suggests that this method is not particularly suitable to this study species. Yet Pouillevet et al. (2017) compared different methodologies for extracting primate parasites eggs and cysts from faecal samples. Two of the parasite species extracted are the same as the species seen in Tsaobis: *Entamoeba coli* and *Balantidium coli*, and whilst the zinc sulphate McMaster flotation showed the best results for extracting protozoan cysts, this was closely followed by the sedimentation method (Pouillevet, 2017). The specific methodology of this sedimentation technique differed from the modified formal-ether concentration technique. However, these findings illustrate the accuracy of using sedimentation as a tool for detecting parasites.

Other considerations with this method of sample collection is that parasite counts may be influenced by the consistency of faecal samples, where the wetter the consistency the more diluted the sample. For example, Ravasi (2009) included a multiplication factor against five different categories of faeces consistency. Whilst I recorded the faeces consistency for the parasite samples collected in 2014-2015, this multiplication factor was not included in the analyses here. For many of the analyses in this thesis I explored the associations with the presence or absence of the parasite species, or parasite species richness. In cases where I included parasite abundance or incidence, the output of parasites were important in a raw form to assess the output of parasites per faeces, which ultimately will be a key determinant of onward transmission potential for that parasite from that host.

Remote sensing: normalised difference vegetation index

In order to assess landscape-level patterns of environmental variation over space and time, i.e. between troop home ranges and across seasons, I used a satellite measure: the normalised difference vegetation index, NDVI. NDVI is a remotely sensed proxy for environmental productivity, estimated through determining the 'greenness' of an area (Pettorelli, 2013). As such, it is an indicator of vegetation cover, and therefore the availability of food for the baboons. The higher the value the more productive the area, and it has been previously shown to indicate habitat quality for baboons (Zinner et al., 2001). As a measure

of vegetation cover, NDVI also indicates the availability of potential parasite microhabitats, and, where vegetation cover is strongly dependent on rainfall (as it is at Tsaobis), the amount and distribution of recent rainfall events and the associated wetness of the environment.

To calculate the variation in NDVI experienced by the two study troops, I determined their home ranges across all years. To do this, I first took all the GPS locations of the two troops' positions, taken every 30 minutes by observers during the 2005-2017 study seasons (totalling 31,575 points for L troop; 30,087 points for J troop), and used kernel density estimates (KDE) to calculate the 99.9% isopleth home ranges with the R package adehabitatHR (Calenge, 2019). I then added a 1-km border to include habitats that are available to the troops that might also be used in between field seasons. I then extracted the MODIS NDVI values for the area using Google Earth Engine; with the MODIS data set at a 250 x 250 m spatial resolution and a 16-day temporal resolution (MODIS 13Q1 v006; Didan et al. 2015). Only the NDVI falling into the home range were extracted for each troop, and only one value for the month was used (based on whichever was closest to the middle of the month).

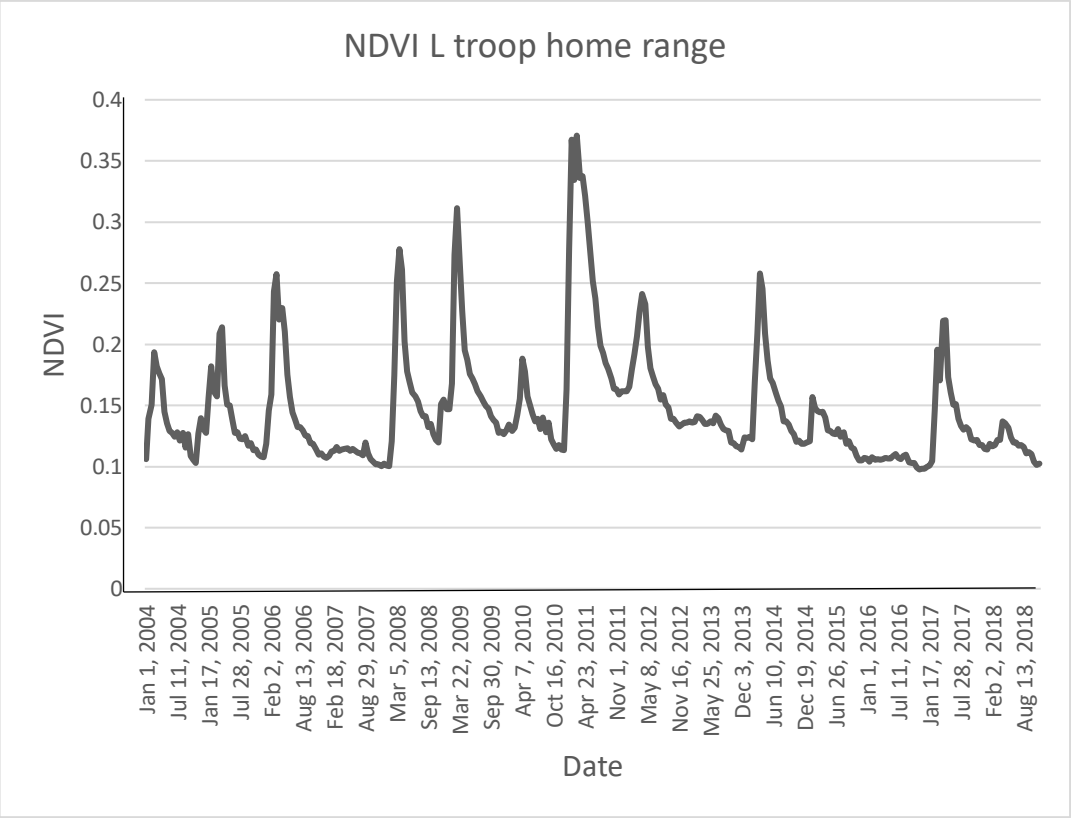


Figure 4.8. Monthly variation in NDVI in the home range of troop L between 2004-2018.

The NDVI patterns that emerged show strong seasonal fluctuations, coinciding with the summer rains at Tsaobis, and further demonstrating the substantial variation that occurs between years (Fig. 4.8). Specifically, the NDVI data clearly capture the record rain year in 2011, as well as the severe drought in 2007 and more recently in 2016 and 2018. This figure shows the pattern for troop L, but an identical pattern is seen in troop J, indicating that there is very little variation in the quality of the home ranges between the troops – as might be expected, given the substantial troop overlap (see Fig. 4.1A). Note that the NDVI troughs in the austral winter would be lower than observed here, if it were not for the perennial green vegetation of the riparian woodland and shrubs along the Swakop River, where the baboons forage during the winter months.

These data are used as a measure of environmental variation in Chapters 5, 6 and 7. Further details are provided in those chapters.

CHAPTER FIVE

Movement behaviour and gastrointestinal parasite infections in wild baboons: ecological traps and landscape of disgust

ABSTRACT

Where a host moves within its home range dictates the likelihood of its exposure to parasites. Not only can spatial heterogeneity of landscapes shape the movement of a host, it can shape the survival of parasites within the environment, and thus impact parasite transmission through multiple routes. However, hosts can exhibit avoidance behaviours in order to reduce parasite transmission. Here I explored how baboon movement across a heterogeneous landscape dictates parasite transmission, and whether baboon troops avoid habitats that risk parasite exposure. Firstly, I explored the spatial heterogeneity of parasites. I found that parasite distribution from defecation is determined by host ranging behaviours, and that woodland habitats provide shaded conditions that may increase parasite egg/cyst survival. Secondly, I explored how repeatedly visiting habitats can influence parasite infection risk in the following months. I found that repeated habitat use in general was associated with a subsequent decrease in directly transmitted parasite prevalence, however, repeated visits to woodland habitats specifically was followed by an increase in directly transmitted parasite prevalence. Finally, I explored whether baboon troops avoided revisiting habitats when parasite presence or burden was high. In these troops, as directly transmitted parasite infection increased, the amount of revisiting of habitats decreased. Consequently, host movement and parasite distribution in the environment influences transmission, but baboons appear to employ an anti-parasite behavioural strategy to reduce high infection risk.

INTRODUCTION

Parasites are limited in their dispersal capabilities (Dougherty et al., 2018; Milner-Gulland et al., 2004; Ostfeld et al., 2005). For this reason, the extent of movement of the host dictates the likelihood of its exposure to parasites, either through revisiting areas where the host has previously spread parasites or moving into areas where other hosts deposit parasites. Depending on the parasite's transmission mode, contact needs to occur between the susceptible host and either infective conspecifics, the environment where infective conspecifics have deposited parasites, or intermediate hosts (Daversa et al., 2017). Many gastrointestinal parasites are transmitted through the faecal matter of an infected individual, and once within the environment the eggs or cysts (the infective stages of macro- and microparasites respectively) become infectious and then typically enter their next host through the oral route, potentially a considerable time later, depending on the persistence of the egg or cyst in the environment.

The spread of many gastrointestinal parasites is therefore dependent on the interactions of the host with its habitat (Real & Biek 2007). In a heterogeneous landscape, the movement of animals may be clustered around key resources such as food and water, shelter, and mating sites such as leks (Berger-Tal & Bar-David, 2015). How an individual animal or social group uses a landscape can be defined as its utilisation distribution: a probability distribution of the likelihood of the animal or group occurring at a point in space. From the utilization distribution emerges the home range, the area that an animal or social group exists in for most of its time, excluding rarer movement events (Burt, 1943). Changes in host home range as a result of changes in resource distribution, and their impact on parasite transmission, have been explored through individual-based models (Bonnell et al., 2016; Leach et al., 2016; Nunn et al., 2014). The overall findings of these models is that resource quality and distribution influence the likelihood that susceptible hosts are exposed to environmentally transmitted parasites. Models of primate movement and parasite transmission indicate that the intensity of range use, more so than home range overlap, is positively associated with parasite prevalence within a troop (Nunn, 2011). However, behaviour is not the only contributing factor. Nunn et al. (2014a) found that whilst the intensity of landscape use was important in contributing to parasite transmission, so too was the degree of parasite survival in the soil.

Landscape heterogeneity can be a key driver of infection dynamics, by providing microclimatic conditions that influence parasite survival and thus the spatial distribution of parasites (Ostfeld, 2005; Wilson, 2002). Landscape heterogeneities in temperature and moisture have long been known to influence parasite egg survival (Brown, 1927). Whilst parasite eggs and cysts are encapsulated to protect against environmental conditions, high temperatures and low moisture promote desiccation of these cells. Additionally, experimental studies indicate the importance of vegetation in shaping the microclimates that promote parasite egg survival (Larsen & Roepstorff, 1999; Rose & Small, 1980). The higher survival rates of helminth eggs in areas of high vegetation cover has been shown to mitigate against the desiccation of faeces despite the fact that vegetation cover did not alter the temperature the faeces were exposed to (Berbigier et al., 1990).

The importance of the spatially heterogeneous survival of parasites has been shown to be important in shaping a host's risk to exposure in empirical and experimental studies. In an environmentally transmitted pathogen, *Batrachochytrium dendrobatidis*, removal of

habitats that posed a higher risk of parasite transmission than others led to a decrease in the prevalence and intensity of infection in alpine newts (*Ichthyosaura alpestris*) (Daversa et al., 2018). Individual-based modelling of landscape microclimates on the survival and subsequent transmission of *Trichuris* spp. eggs infecting red colobus monkeys (*Procolobus rufomitratus*) suggest that only a few locations were likely to act as a source of parasites (Bonnell, 2016). Consequently, transmission to the host becomes reliant on the movement behaviour of the host (Bonnell, 2016), especially in relation to these source areas which can be considered hotspots for transmission (Paull et al., 2012). However, observational studies are often unable to tease apart the multiple roles which spatial heterogeneity may have in shaping parasite transmission (Brearley et al., 2013; Morgan et al., 2004).

The spatial distribution of faeces within a host's home range can either be dispersed randomly, resulting in a similar spatial pattern to the animal's movement behaviour, or dispersed at localised sites, i.e. in dung heaps or latrines. Selective defecation or elimination allows the host to control the input of parasites into their host range. Environmentally-transmitted parasites, limited in their ability to disperse, are restricted to the location of defecation, with Ezenwa (2004a) noting that in African bovids the environmental contamination of gastrointestinal parasites was higher closer to their faeces. Selective defecation may assist in avoiding infection by keeping parasite contamination away from frequently foraged areas. Parasite avoidance through selective defecation has been noted in primates, with red howler monkeys (*Alouatta seniculus*) defecating in specific locations, using latrines that are away from vegetation that they might use to travel across or consume (Gilbert, 1997). However, this defecation strategy is certainly not the rule in primates, with mangabeys (*Cerocebus albigena*) showing no evidence of avoiding defecating on food(Freeland, 1980). When comparing domestic horses in pastures to free-living horses, those that are unable to roam long distances show evidence of latrine use in contrast to the behaviour of free ranging horses, indicating parasite avoidance behaviour may be more likely in situations where exposure to parasites is high (Lamoot et al., 2004).

Recursive ranging behaviour and the creation of ecological traps

Freeland (1976) proposed that repeated host visitation to areas of a home range increases the faeces in that area, which in turn increases the parasites in those environments. Evidence of this is seen in bovids where individuals that are less territorial and more gregarious harboured more parasite species than more territorial and solitary species (Ezenwa, 2004).

Additionally, a meta-analysis across 119 primate species found that range use intensity increased parasite richness (Nunn & Dokey, 2006). The distribution of resources is a key driver of this, often encouraging repeated revisits (recursive movements) to a resource (Berger-Tal, 2015). When an Ebola virus outbreak occurred in lowland gorilla (*Gorilla gorilla gorilla*) populations, transmission of the virus appeared to occur across social groups (Bermejo et al., 2006). Since transmission of Ebola requires close contact, a rare event in gorilla groups, it appears that key features of the landscape were most likely encouraging contact. Specifically, seasonally fruiting trees are visited by many gorilla groups simultaneously, and represent a possible 'transmission island' for the virus (Caillaud et al., 2006). The type of resource also matters in terms of shaping movement behaviours. Elephants were more likely to show recursive movements towards resources that were likely to have replenished or that were able to sustain repeated visits (English et al., 2014). In addition, the overlap involved in the recursive movement patterns of travelling between these locations can also be important (Benavides et al. 2012).

The input of parasites into the environment can exacerbate heterogeneities across the landscape, providing a landscape of parasite sources and sinks. An accumulation of faecal material may also provide an input of nutrients into the environment, which in turn promotes the growth of vegetation that encourages the hosts to revisit (Smith et al., 2009b). Similarly, carcasses have been shown to encourage localised plant growth in locations where the spores of anthrax are deposited from the same carcass (Turner et al., 2014). Such patterns perpetuate the cost-benefit trade-off between nutrient consumption and parasite avoidance in omnivores and herbivores. However, when parasites are undetectable to the host, the high quality of resources in these areas can attract hosts irrespective of the high density of parasite eggs and cysts, leading them into an ecological trap (Leach, 2016).

Avoiding ecological traps and the landscape of disgust

Whilst the movement of the host is shaped by its resources, the risk of encountering parasites can also play a role in determining its decision about where to forage, provided that such risks can be detected. In fact, alteration of behaviour patterns by the host is a key strategy for managing exposure to pathogens (Hart, 1990), and parasite avoidance may be more effective than the immune response as a method of managing infections (Daly & Johnson, 2011). However, there is a cost to avoiding high-risk habitats. In decisions about where to forage or utilise resources, individuals will need to trade-off the quality of the resource (e.g.

its nutritional content) with the associated risk of exposure to parasites (Hutchings et al., 2006). In Japanese macaques (*Macaca fuscata fuscata*), for example, parasite avoidance behaviours are stronger when the nutritional benefit of the food is lower (Sarabian & MacIntosh, 2015). One way in which potential hosts might minimise the risk of infection to parasites is through the recognition and avoidance of cues associated with this risk, leading to a so-called 'landscape of disgust'. Mirroring the ecological effects of the 'landscape of fear' phenomenon, where predator avoidance shapes the behaviour of prey, the 'landscape of disgust' may shape the ecology of potential parasite hosts (Buck et al. 2018; Weinstein et al. 2018). Using cues that prompt a feeling of disgust, such as faeces or body fluids, an animal may be motivated to move away from areas where the risk of parasite infection is high.

Certainly, habitat choice and selective foraging are potentially important methods for avoiding environmentally transmitted protozoan and helminth parasites (Thieltges & Poulin, 2008). Some animals may even migrate long distances to avoid parasites in the environment (Ltizer et al., 2011). Seasonal migrations of reindeer (*Rangifer tarandus*), for instance, result in susceptible hosts moving away from parasitic fly larvae (*Hypoderma tarandi*) that are developing in the soil, reducing their risk of infection in comparison to non-migratory populations living in the same environment (Folstad et al., 1991). Similarly, dominant groups of zebra (*Equus burchelli*) at risk of ingesting anthrax exhibit partial migration away from high-risk locations at the cost of accessing high-quality habitats, with lower-ranking groups left to graze in high-risk areas (Zidon et al., 2017). While we cannot infer whether migration behaviour is entirely driven by parasite avoidance, it does illustrate the benefits incurred from this behaviour.

Such avoidance behaviours rely on a host species being able to sense and respond to cues of parasites within the environment (Sarabian et al., 2018), .e.g., detecting and adopting a disgust response to the presence of faeces. In the case of the latter, Japanese macaques (*Macaca fuscata fuscata*) avoid consuming wheat when associated with both real and replica faeces (Sarabian, 2015). Likewise, captive chimpanzees (*Pan troglodytes troglodytes*) show behavioural avoidance when near cues associated with bodily products (Sarabian et al., 2017), and sheep avoid foraging in areas where there is faeces, notably showing equal disgust regardless of the degree of infection the faeces is carrying (Cooper et al. 2000). This pattern of behaviour is also seen in free-living ungulates where wild Ibex (*Capra ibex*) avoid foraging in close proximity to faeces (Brambilla et al., 2013).

Different factors can shape the extent to which a host is willing to avoid the risk of parasite transmission over the benefits that might be received by utilising these areas. For example, for multiple species that are attracted to seeds in racoon faeces, the avoidance responses were higher for those species that shared parasites with racoons (Weinstein et al. 2018). This illustrates that a host's susceptibility to a parasite may influence the amount of avoidance behaviour it is likely to adopt (Hart, 1990). Furthermore, there is evidence that the avoidance of repeatedly used habitats is higher when parasite egg and cyst expulsion is higher, as seen in mandrills (*Mandrillus sphinx*: Poirotte et al. 2017). Similarly, once sheep are infected with gastrointestinal parasites they are much more likely to avoid areas with faeces (Cooper, 2000), and wild mice infected with parasites were less likely to spend time in areas that were contaminated with faeces (Hou et al., 2016). These examples suggest that when a host is infected with parasites the cost of further exposure increases the degree of parasite avoidance behaviour that they exhibit.

Aims

In this chapter, I explore how host movement behaviour in wild chacma baboons interacts with landscape heterogeneities to influence their parasite infection risk, and whether behavioural avoidance by the host is evident as a means of reducing infection risk. I begin by identifying whether infection risk is likely to be heterogeneous in the landscape, and identify the highest risk habitats, assuming that a build-up of infectious parasites in the soil is dependent on the conditions being suitable for the persistence of these infectious stages (Bonnell, 2016; Nunn, 2014; Ostfeld, 2005). I then go on to test three hypotheses relating to defaecation behaviour, movement patterns, and parasite infection risk. Specifically, Hypothesis 1 (H1), that the baboons will defecate in a non-random way that may reduce infection risk; (H2) that recursive ranging behaviour by the baboons increases their risk of infection, on the assumption that areas of intensive use are likely to accumulate infectious parasites in the soil (Robertson et al. 2013; Nunn & Dokey 2006; Leach et al. 2016), creating an ecological trap; and (H3) that infected baboons avoid areas associated with a higher infection risk in accordance with a landscape of disgust (Hart, 1990).

To test these hypotheses, I analysed the ranging behaviour and gastrointestinal parasite infection status of wild chacma baboons (*Papio ursinus*). Baboons are terrestrial omnivores, and therefore prone to infections from parasites transmitted via the environment. The directly transmitted gastrointestinal protozoa, primarily consisting of *Balantidium coli* and

Entamoeba species, are transmitted through faecal contamination via water and soil (Hausfater & Meade, 1982; Karanis et al., 2007). As the cysts are highly exposed to environmental conditions, the heterogeneity of the microclimate across the landscape will influence where these infectious stages can persist (Paull, 2012; Smith, 1999). The two helminth species (*Physaloptera caucasia* and *Streptopharagus pigmentatus*) in this study system are indirectly transmitted, and are included in the analyses as 'controls'.

METHODS

This study was carried out at Tsaobis Nature Park, Namibia, and focussed on two troops of wild chacma baboons over the period 2005-2015. The study period encompassed 9 field seasons ranging in length from 2-7 months. Troop members were individually recognisable and habituated, and individual age was either established using known date of birth or taken from dental examination. For further details on the study site and study population, see Chapter four: methods.

Collection of baboon movement data

The movement patterns of the two study troops were recorded throughout the 2005-2006 and 2009-2015 field seasons. Each morning the observers arrived at the sleeping cliff and throughout the day they used GPS (Global Positioning System) to record the coordinates of the troop's position at 30-minute intervals until dusk, when the baboons ascended onto their sleeping cliff. These coordinates were recorded from the centre of the troop when the GPS accuracy was ≤5 metres.

Collection of faecal samples and defecation location data

Faecal samples were collected and analysed across the 2005-2006 and 2009-2015 field seasons, following the methods described in Chapter 4. In total, 1034 faecal samples contributed to the avoidance analysis (J troop = 578; L troop 456), 1634 (J troop = 970; L troop = 664) and 1145 (J troop = 654; L troop = 491) samples contributed to the one month and two month lagged analysis respectively. In 2014-2015, GPS points were also taken to record the defecation location of all faecal samples collected. In addition, GPS points were also used to record the location of defecation events during behavioural data collection ('focals') regardless of whether the faeces were sampled. As the focals were evenly distributed

throughout the day (see Chapter 4) these latter location data were free of any potential observer bias that might affect the location data of the collected samples (if observers were more likely to focus on faecal sample collection at certain times of the day).

Mapping Tsaobis habitats

The Tsaobis landscape comprises two primary habitats: the Swakop River, which supports perennial riparian woodland vegetation all year round, and the desert hills and plains, which only has green vegetation and associated insect life, including orthopterans, during and after the austral summer rains (see Chapter 4 for further details). The baboons preferentially forage on the green herbs, shrubs, and insects of these hills and plains in the austral summer, but forage primarily on the trees and thickets of the Swakop woodlands (hereafter 'woodlands') in the austral winter, spending time in the hills and plains only as necessary for sleeping cliffs and waterholes.

In order to map the distributions of the woodlands and non-woodland habitats, I used supervised classification using the random forest classifier (Breiman, 2001), a form of machine learning. Supervised classification requires training data to train this classifier, and tree location was established using Normalized Difference Vegetation Index (NDVI) data from 2016 as calculated from the Sentinel-2 bands 8 and 5. That is, on the satellite image of the study site (Fig 5.1A) I identified some of the tree locations, and non-tree locations, as the training data for the classifier to identify the other areas of the habitat with the same properties, on the basis of the NDVI data. Sentinel-2 satellite (Copernicus Sentinel data 2017) were used as these remotely sensed data are at a spatial resolution of 10 metres. From this I could determine tree locations at very low densities (see Fig. 5.1B). Tree locations are stable across years at Tsaobis, hence I can create one habitat map for the whole study period from this year. Access to remotely sensed data, and the supervised classification analysis, were completed using Google Earth Engine (https://code.earthengine.google.com; Gorelick et al. 2017). A reduction in resolution was necessary to manage the processing time, so the habitat map was scaled down by a factor of 10 to produce the final habitat map (Fig. 5.1C).

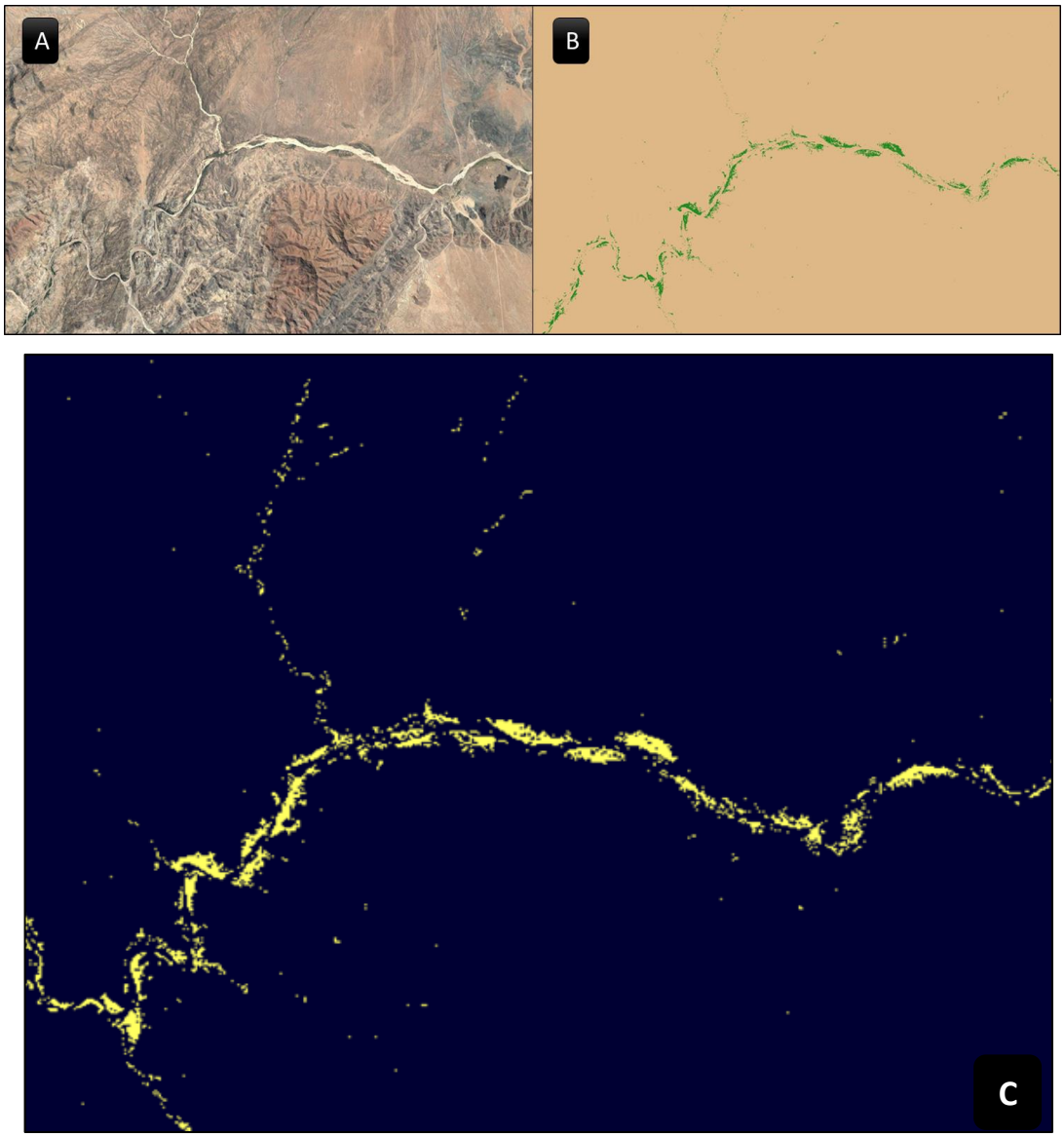


Figure 5.1. Comparison of (A) the satellite image of the study site and (B) the habitat map of supervised classification of trees [green = trees; light brown = other vegetation type]. Images produced through Google Earth Engine. (C) The final habitat map of woodland (yellow) and non-woodland (blue) areas as determined through supervised classification, with a reduced resolution.

Provisioning

During several periods over the 2005-2006 and 2009-2015 field seasons, the baboons were provisioned. This involved creating a short-lived but artificially high-quality, localised, food resource outside the Swakop woodland during the austral winter, using loose corn kernels ('mielies') spread over a large area for periods of 1-3 weeks at fixed locations (in advance of trapping events and during foraging experiments). Provisioning usually occurred at different weeks for each troop. To control for the possible effects of such provisioning on the ranging

behaviour of the troops, I calculated the number of days the troop was provisioned across each two-month period in the analysis (see below). If only one month was provisioned, I considered that the total number of days provisioned was 0.

Assessing environmental variation

The seasonal changes in the environmental conditions were similarly assessed using NDVI. NDVI is a proxy for the environmental productivity, estimated through the determining the 'greenness' of an area (Pettorelli, 2013). I use NDVI as a general measure of seasonal environmental variation, to allow for the possibility that NDVI may not only reflect food availability for the baboons, as the greenness reflects vegetation cover, but also the potential abundance of parasites if, for example, parasites benefit from higher 'greenness' due to the greater availability of water, shade (from the vegetation), and damp microclimates (in the vegetation). For further details of how NDVI is quantified, see Chapter 4.

Quantifying habitats for parasite eggs/cysts

Variation in microhabitat temperature

I measured the temperature of shaded and uncovered soil in both woodland and non-woodland habitats for three months in the 2014 field season (October to December). This range of temperatures only captures the early austral summer, and is therefore not representative of the full year, although it does represent an extreme season. In all cases, ThermaData Loggers (Electronic Temperature Instruments) were placed just below the soil surface (n = 7 locations), and these recorded the temperature on an hourly basis. Using four Gaussian general linear models (GLM) I compared the mean, maximum, minimum, and range of the temperatures with the location substrate type (sand vs. gravel), and whether the location was shaded or exposed, and the month.

Variation in shade

The shade availability of woodland and non-woodland habitats was investigated in 2014. To determine which locations were predominantly shaded, I walked two 50m transects per habitat type, recording the proportion of shade every $2m^2$. The location of these transects were chosen through randomly chosen coordinates (random number generated, restricted to the furthest coordinates of each habitat), and a randomly chosen transect direction

(random number generated to determine degree). These transects were repeatedly walked throughout the day.

Processing of Geographical information system (GIS) data

The GPS data from the ranging locations of the baboons, and the defecation sites of the baboons, were analysed using R v3.3.3 (R Core team 2016). Prior to all analyses the coordinate projection was converted from Geographic Coordinate System to the Universal Transverse Mercator (UTM) projection for zone 33k (Namibia), using the SpTransform function from the package rgdal (Bivand et al., 2017). Any months with fewer than 300 data points (i.e. less than half the expected data collection per month) were omitted from the analyses. A summary of the years and month where GPS data and faecal samples were collected are listed in Appendix 2, Table S5.1.

Testing for non-random patterns of defaecation (Hypothesis H1)

To test the hypothesis that baboons do not defecate at random, I compared the utilization distribution (UD) of the baboon ranging patterns with the hotspots of defecation events using kernel density estimates (KDE). If the hypothesis is correct, the two distributions should deviate from one another, but if the baboons defecate at random the two distributions should coincide. The home range analyses used functions from the adehabitatHR package (Calenge, 2019) in R. I produced monthly home ranges, and hotspots of defecation locations, using kernel UD with the reference bandwidth smoothing parameter (h_{ref}) from the href function. The reference bandwidth was used due to the small sample size of the defecation points. As this bandwidth tends to over-smooth GPS data (Walter et al., 2011) it is preferable for these data as the larger *h* value allowed us to detect patterns of hotspots. I then compared the monthly UD against the hotspots using the kernel overlap function to calculate the Volume of Intersection (VI) (Seidel, 1992) and Bhattacharyya's affinity (BA) (Bhattacharyya, 1943) for 95% isopleths. VI and BA are measures of similarity between two probability distributions. Both indices range from zero (no overlap) to one (matching UDs).

Quantifying repeated habitat use

Recursive ranging behaviour was quantified across all habitats and for woodland habitats only. In the first case, to assess repeated habitat use across all habitats, the home range and UD were created for each month. I used Movement-based Kernel Density Estimations through the Brownian Bridge approach (BRB/MKDE) with the “BRB” function,

incorporating movements trajectories of the baboons (Benhamou, 2011; Benhamou & Cornélis, 2010). Then, to compare the overlap of the UDs over each month, I used the Utilization Distribution Overlap Index (UDOI) (Fieberg & Kochanny, 2005) to compare the UDs for all habitats across months. In the second case, to assess repeated habitat use within woodland habitat, the home range and UD restricted to this habitat were created for each month. Using the home range and UDs created for each month I overlay woodland locations and removed the UD that fell outside these areas. I then compared the overlap within woodland habitat between months using the percentage of overlap (HR) (Kernohan et al., 2001). This resulted in an overlap index between 0-1 (between no overlap and complete overlap) for each month to indicate the degree of revisitation occurring in the woodlands in relation to the previous month.

Statistical analysis

All the following analyses were run using R v3.3.0 (R Core Team, 2019) with the packages 'lme4' (Bates et al., 2015) and 'MuMIn' (Barton, 2016).

Testing for an effect of recursive ranging on infection rates (Hypothesis H2)

To test whether the infection status of the baboons was influenced by repeated habitat use (temporal range overlap), I used generalized linear mixed models (GLMMs). I assessed individual infection status for five different parasite species or species groups using presence/absence, fitted with a Binomial error structure. These species or species groups comprised the protozoan *Balantidium coli*, medium amoeba and small amoeba, and the two helminths *Streptopharagus pigmentatus* and *Physaloptera caucasia*. For each of these five models, the key predictor variables were the overlap across all habitats (UDOI) and the proportional overlap in woodland habitat only (HR) over two consecutive months. I also controlled for the potential influence of individual characteristics on infection status, namely sex and age (as a second-order polynomial, following (Benavides et al. 2012), and environmental variation, by including year and the mean NDVI for the two successive months across which overlap was measured. The identification of each baboon was also included as a random intercept term to account for the pseudoreplication of repeat-sampling individuals. I had intended to include two further fixed effects: troop ID to control for potential intertroop differences, and the total NDVI for each year as a more direct measure of interannual

environmental variation than simply year. In the first case I had to exclude troop ID because the models failed to converge. This was likely because this variable is only at 2 levels. My inability to control for troop ID should not lead to any problems with pseudoreplication (both troops contributed approximately the same number of points to the analysis), but it does mean I'm unable to assess whether the two troops showed any differences in their patterns of behaviour or parasite burdens. In the second case, when I tested for multicollinearity between the fixed effects using a Pearson correlation matrix, both NDVI for the two overlapping months, and NDVI for the 12 months prior to the overlapping months were highly correlated ($|r| > 0.7$). As this exceeds the acceptable threshold for collinearity (Dormann, 2013), I did not include the latter. I also considered two possible time frames over which an effect of repeated habitat use on individual infection status might be seen, to allow for the possibility that an effect would only be seen either in the second of the overlapping months (Lag 1) or in the month after the overlapping months (Lag 2). Thus two models were run for each of the five parasites, leading to a total of 10 models.

Testing for avoidance of high-infection-risk areas (Hypothesis H3)

To test whether high levels of parasite infection were associated with the avoidance of repeated habitat use, I used linear models (LMs). Two models were run, the first to explore the effects of infection status on recursive behaviour in all habitats, the second to explore the same effects in woodland habitats only. As response variables, the proportion of monthly home range overlap (UDOI) was log transformed, and the proportion of monthly home range overlap within the woodland habitat (HR) logit transformed (Warton & Hui, 2011), to approximate normality and permit the use of a Gaussian error structure. The fixed effects included the parasite abundance for the same three protozoan species or groups (*B. coli,* medium amoeba, and small amoeba) and two helminth species (*S. pigmentatus*, *P. caucasia*) as above, using rank scores of abundance in the former and absolute egg counts in the latter (see Chapter 4 for further details). Additional fixed effects included with the mean NDVI across the two overlapping months, whether the baboons were provisioned in both months, troop, and the year. Collinearity was tested between all these variables using a correlation matrix (Pearson), and none were above the standard $|r|>0.7$ threshold (Dormann, 2013).

Model selection

I used the information-theoretic approach for model selection (Burnham, 2002). I considered all possible combinations of fixed effects and compared the fit of each model through Akaike's information criterion (AICc), with the R package MuMIn (Barton, 2016). All models within Δ6 AICc units of the best supported model were selected. I then used the 'nesting rule' to exclude those models that were more complex versions of nested (simpler) models in this set with better AICc support. This was because AIC often selects unnecessarily complex models, and simpler versions of the models with better AIC were preferred over more complex models (the nesting rule: Richards 2008; Arnold 2010). After the application of this nesting rule, if more than one model remained in the top set then model averaging was used to calculate the parameter estimates and standard errors of a final composite model. This composite model was determined using the model.avg function in the MuMIn package with full-coefficient modelling. Any variables that had 95% confidence intervals crossing zero were deemed inconclusive (du Prel, 2009).

RESULTS

Identifying high-infection-risk habitats

The identification of the habitats that provide a higher probability of parasite survival was determined through assessing which habitats had the highest portion of shade, and the degree to which shade alters microclimates. In the first case, the woodland habitat had the largest proportion of shade due to the presence of trees (Fig. 5.2). The limited shade available in the hills (non-woodland habitat) was mostly due to the aspect of the hills, as well as the few dwarf trees present in this habitat. Only 10% of non-woodland habitat is shaded, whereas 36% of woodland habitat is shaded.

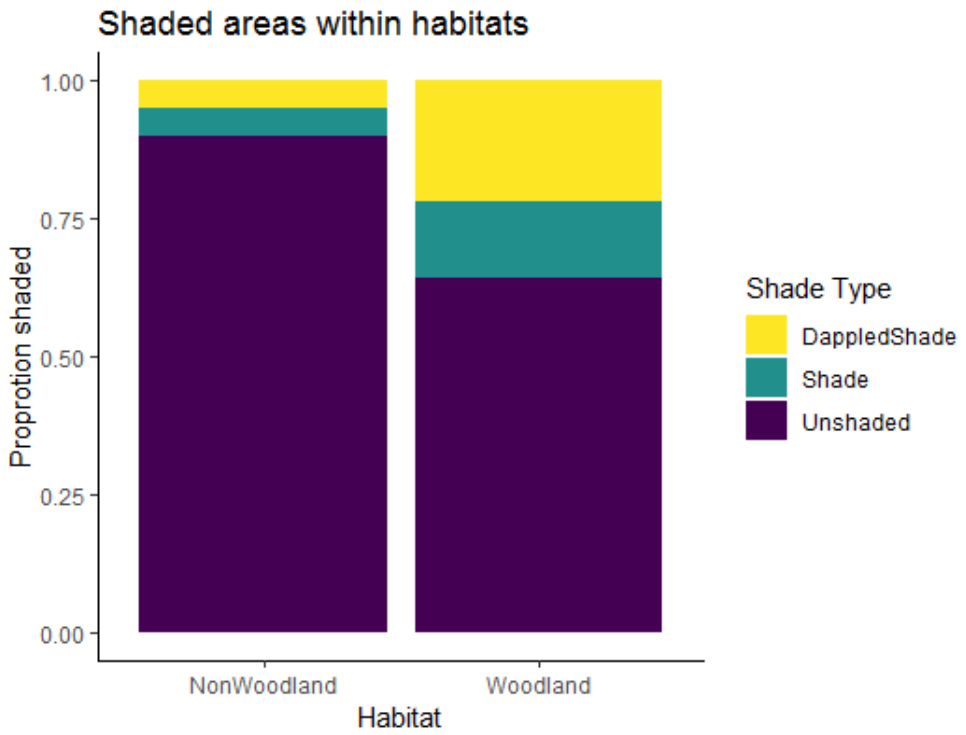


Figure 5.2. The proportion of shade along transects of the woodland habitats and of non-woodland habitats.

In the second case, soil temperatures ranged from 8.4°C to 70.7°C with a mean of 29.0°C. There was no statistically significant difference between substrate types (sand and gravel) according to their mean, maximum, minimum, or range of soil temperatures (GLMs: all $p>0.05$). Nor were there significant differences in the soil temperatures across the months (October to December). However, soil temperature was significantly lower in shaded versus unshaded locations (means: 27.7°C compared to 31.8°C, respectively). This was true not only for the mean but also the maximum, and range of temperature ($p<0.01$, $df=17$, in all cases). The minimum temperature showed a similar trend but did not quite achieve statistical significance ($p=0.07$, $df=17$).

Altogether, these results suggest that woodland habitats are more shaded and exhibit lower soil temperatures, which is likely to promote the survival of parasite cysts and eggs. This is likely to make woodland a higher risk habitat than the more exposed desert hills and plains.

Do the baboons reduce infection risk by selective defaecation? (H1)

To assess whether the defecation patterns of the baboons deviated from their wider ranging patterns, in support of H1, or coincided with their ranging patterns, contrary to H1, I

compared the overlap between the monthly home ranges with the monthly location of defecation events, as determined through the overlap indexes (Volume of Intersection, VI, and Bhattacharyya's affinity, BA) between the utilization distributions (UD) and the defecation hotspots, across months (Fig. 5.3). The mean value across all months (n=8) were VI = 0.73 (J troop: range = 0.56-0.86; L troop: range = 0.61-0.80) and BA = 0.86 (J troop: range = 0.72-0.93; L troop: 0.77-0.91). These figures indicate a high degree of overlap, even in those months when VI and BA were at their minima, contrary to H1.

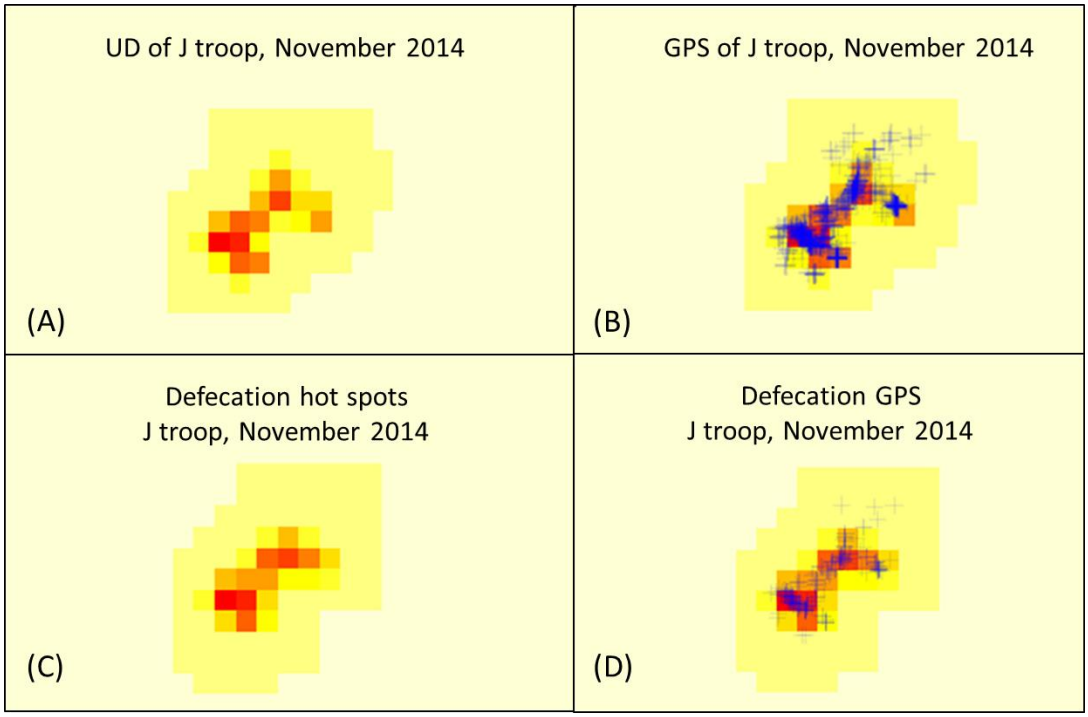


Figure 5.3. The home ranges and defecation hotspots of one of the two study troops (J) in November 2014. The left hand panels show intensely used areas (A) and high frequencies of defecation events (C), in red. On the right hand panels, the same images are shown but with the GPS points of troops (B) and defaecations (D) superimposed as blue crosses. Note that there is a high degree of coincidence between the UDs (A, B) and the defecation hotspots (C, D).

Does recursive ranging behaviour create an ecological trap? (H2)

The models testing whether the presence/absence of parasite species in the host was associated with prior recursive behaviour, i.e. the lagged overlap of ranging across months, are summarised in Table 5.1 (further details are provided in Appendix 2, Table S5.5). In the case of recursive ranging behaviour across all habitats, following periods of greater recursion the frequency of infections with *B. coli* and medium amoeba declined two months later, and for small amoeba declined one month later (see Figs. 5.4A; 5.5A). The same trends, but

inconclusive, were also observed with small amoeba, *P. caucasia*, and *S. pigmentatus* two months later, and *S. pigmentatus* one month later. These patterns are contrary to the hypothesis that repeated habitat use creates an ecological trap (H2). In contrast, in the case of recursive ranging behaviour in woodland, following periods of greater recursion the frequency of infections with *B. coli* and small amoeba increased after one month (see Figs. 5.4B; 5.5B). The same trend, but inconclusive, was observed with *S. pigmentatus*. These woodland results support H2.

Only two control variables appeared consistently: year and NDVI. In the case of NDVI, there was a consistent trend for parasite presence to be greater following dryer periods, although these results were only conclusive for medium amoeba (after one month), small amoeba (after one and two months) and *P. caucasia* (after one month).

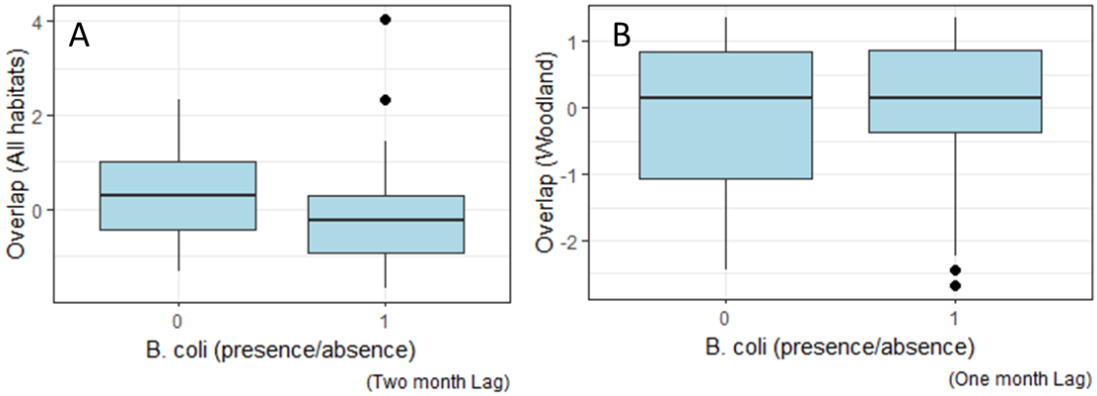


Figure 5.4. Box-and-whisker plots of the raw data showing the mean (solid bar), the upper and lower interquartile ranges (top and bottom of box), the full range of values (whiskers), and outliers (individual points). The association between the presence/absence of *B. coli* after repeatedly visiting (A) all habitats, and (B) woodland habitats.

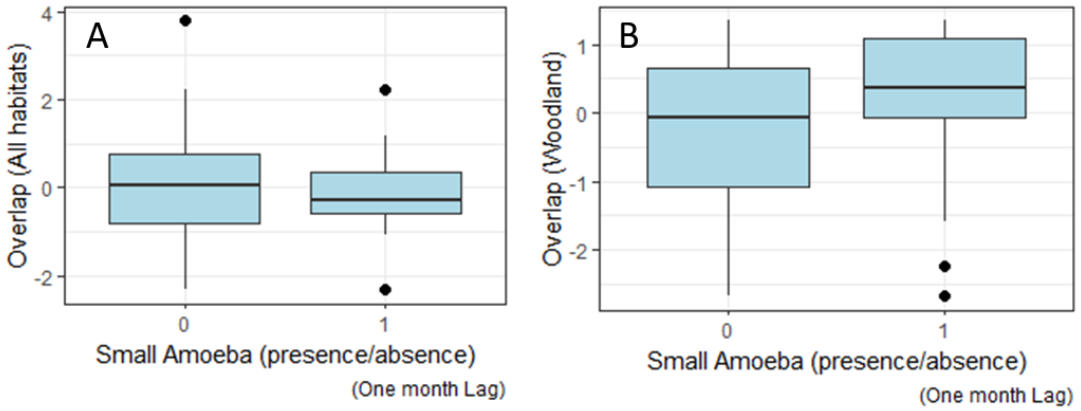


Figure 5.5. Box-and-whisker plots of the raw data showing the mean (solid bar), the upper and lower interquartile ranges (top and bottom of box), the full range of values (whiskers), and outliers (individual points). The association between the presence/absence of small amoeba after repeatedly visiting (A) all habitats, and (B) woodland habitats.

	Lag	Overlap		Individual variables				Number of models
		All habitats	Woodland	Age (poly)	Sex	Year	NDVI	
Directly transmitted parasites								
Balantidium coli	1	0	+	0	0	(*)	(–)	4
Balantidium coli	2	–	0	0	0	0	(–)	2
Medium amoeba	1	0	0	0	*	*	–	1
Medium amoeba	2	–	0	0	(*)	*	(–)	2
Small amoeba	1	–	+	*	0	*	–	1
Small amoeba	2	(–)	0	*	0	*	–	2
Indirectly transmitted parasites								
Streptopharagus pigmentatus	1	(–)	(+)	0	0	(*)	0	7
Streptopharagus pigmentatus	2	(–)	0	0	0	0	(–)	4
Physaloptera caucasia	1	0	0	0	0	*	–	1
Physaloptera caucasia	2	(–)	0	(*)	(*)	(*)	(–)	10

Table 5.1. Results of the AICc model selection for analyses of whether recursive ranging behaviour affects subsequent infection status for different parasite species and groups. The + indicates a positive relationship between the variables, whilst – indicates a negative relationship, and 0 indicates no relationship, and * shows a relationship for categorical variables. For those in brackets the coefficients of these relationships crossed zero and are therefore inconclusive results.

Do the baboons attempt to avoid such traps? (H3)

The influence of current infection status on the likelihood of repeatedly revisiting the same ranging area, was tested in two models: for all habitats combined and for woodland only. In the first case, the baboons were less likely to revisit an area when they were more heavily infected with small amoeba (Fig. 5.6B). In the second case, the baboons were less likely to revisit woodland when they were more heavily infected with *B. coli* (Fig.5.6A). Both findings support the hypothesis that heavily infected baboons are more likely to avoid recursive ranging (H3). Similar trends were also observed for small and medium amoeba infections, but these trends were inconclusive. As predicted by H3, this pattern was only observed for parasites with direct transmission; there was no association between the abundance of indirectly transmitted parasites and the repeated use of habitats.

With respect to the control variables, the NDVI, troop, and year were also important predictors, see Table 5.2 (further details of the model selection is in Appendix 2). In the first case, when NDVI was higher, indicating wetter periods with more vegetation growth, the baboons reduced the likelihood of ranging in the same area as the previous month. In the second case, L troop showed a lower rate of revisiting their home range than J troop (Fig. 5.7). Provisioning had no association with the repeated use of either all habitats or woodland alone.

	Indirect parasites		Direct parasites			Environmental				Number of
Overlap	*S. pigmentatus*	*P. caucasia*	*B. coli*	s. amoeba	m. amoeba	Provision	NDVI	Year	Troop	models
All habitats	0	0	0	–	0	0	–	X	X	1
Woodland	0	0	–	(–)	(–)	0	–	X	X	4

Table 5.2. Results of AICc model selection for analyses of whether infection status affects subsequent recursive ranging behaviour. The + indicates a positive relationship between the variables, whilst – indicates a negative relationship, and 0 indicates no relationship, and X shows a relationship for categorical variables. For those in brackets the 5% confidence intervals of these relationships crossed zero and are therefore inconclusive. Reference for categorical troop: L troop.

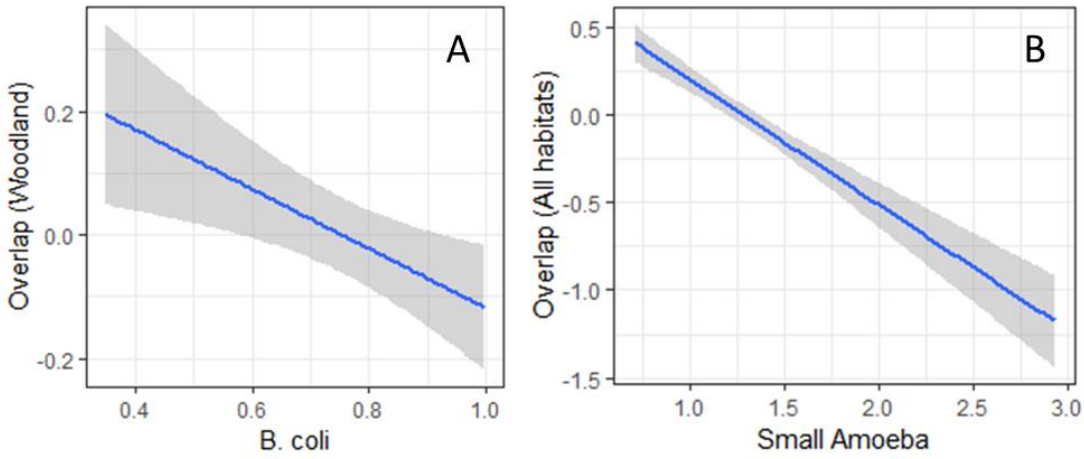


Figure 5.6. Plots showing the association between the parasite intensity for (A) *B. coli* and (B) small amoeba, and the amount a troop revisits previously used habitats (overlap). The fitted line is the mean predicted probability from the mixed effects model, where the shaded area represents 95% credible intervals.

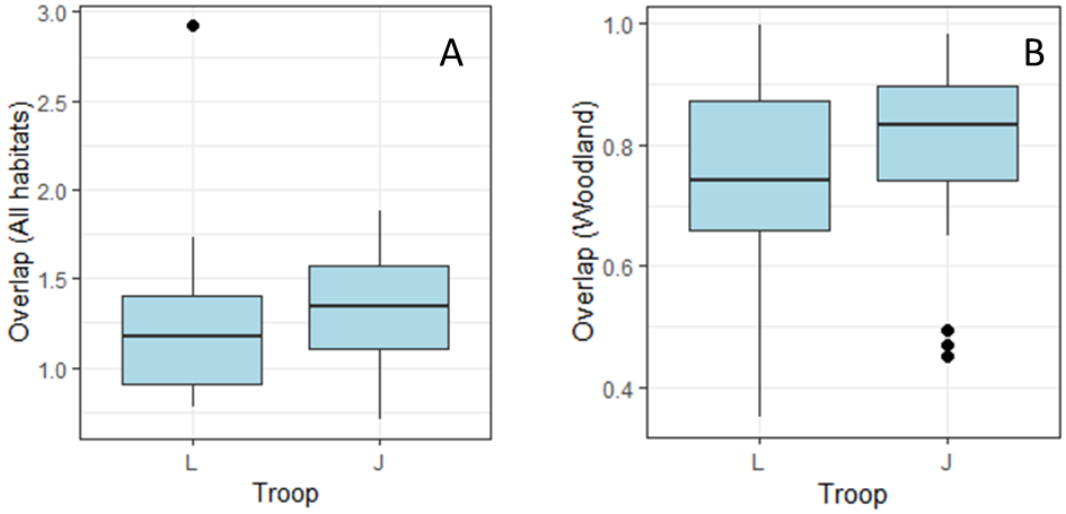


Figure 5.7. Boxplots illustrating the differences in troop overlap for all habitats (A), and for woodland habitats (B).

DISCUSSION

In this chapter I have investigated whether baboons show avoidance behaviours that may reduce their exposure to parasites in the environment. The possible avoidance behaviours included managing the input of parasites into the environment (by selective defecation, hypothesis H1) and avoiding parasite exposure (by avoiding repeatedly visiting home range areas, i.e. recursive behaviour, when risk to parasite exposure is high from high infection expulsion, hypothesis H3). Furthermore, I explored whether recursive behaviours increased the presence of parasites within the troop (hypothesis H2). This was assessed over all

habitats, and specifically within that habitat (woodland) that posed a higher risk of infection due to its lower soil temperatures and being more shaded.

Heterogeneous landscapes may influence the spatial heterogeneity of parasites in an environment in two ways: by influencing host behaviour and by impacting parasite survival. To better understand the latter, I assessed which Tsaobis habitats may be more supportive for the survival and development of parasites. The soil temperatures I obtained were similar to those seen at Kuiseb, another chacma baboon study site not far from Tsaobis, where Appleton and Brain (1995) suggested that if the parasites present in these Namib Desert baboon populations are transmitted environmentally then shade provides a much steadier environment. Indeed, I found shaded ground was significantly cooler than unshaded ground regardless of substrate type (sand or gravel), and was more common in woodland habitat, suggesting that woodland was associated with a higher risk of infection. Shaded locations would be expected to protect cysts from desiccation, as evidenced by temporal changes in cysts surviving in soil (Pierangeli et al. 2003). However, while *B. coli* cysts survival should be favoured by tropical conditions (Schuster & Ramirez-Avila 2008), there is little information from laboratory studies to indicate the critical temperature range of *B. coli* or *Entamoeba* spp. cyst survival. The only information I was able to locate for any of these parasite species came from Chang (1955), who illustrated that as temperatures range from 0-37.5^{o}C, *E. histolytica* cyst survival decreases as the temperature increases, with 7^{o}C enabling cysts to survive for ~28 days, but 25^{o}C limiting cyst survival to 5 days.

One way in which hosts can influence the heterogeneity of infection risk in the landscape is through selective defecation, where the host defecates away from key resources or intensively used areas of its range (Ezenwa 2004). I assessed whether the distribution of baboon faeces matched that of baboon ranging behaviour based on the Volume of Intersection (VI) and Bhattacharyya's affinity (BA) overlap indices. Across months, the values of these indices (VI = 0.73, BA = 0.86) suggested high levels of overlap. For comparison, Kochanny et al (2009) assessed home range overlap in 14 white-tailed deer (*Odocoileus virginianus*) using two different methods and concluded that they generated similar home ranges when VI ranged between 0.49 - 0.78 and BA between 0.67 - 0.94. Our values are therefore indicative of two similar spatial patterns, contrary to the idea that the baboons may show non-random patterns of defecation (H1), and suggest that baboon utilisation distributions are not only indicative of the time a troop spends in a location but also of the

amount of faecal material that is likely to accumulate there and therefore its associated risk of parasite infection in the future.

Building on this finding, I assessed the impact that recursive ranging behaviour in the host has on the subsequent presence/absence of both directly- and indirectly-transmitted parasites, in the second of the two overlapping months in which the recursion occurs (lag 1) and in the following month (lag 2). According to my hypothesis, I expected that recursive behaviour might lead to an increase in directly-transmitted parasites but not in indirectly-transmitted parasites. The results supported this hypothesis (H2): after troops revisited woodland areas the prevalence of *B. coli* and small amoeba increased (in the two month lag and one month lag respectively). Conversely, when troops revisited areas of their home range across all habitats, the prevalence of *B. coli,* medium amoeba, and small amoeba reduced (after one month lag, and two month lag for small amoeba). Additionally, although there was some evidence for associations between revisitation rates and infections with indirectly-transmitted parasites, all were inconclusive. The woodland results are consistent with the earlier analysis of soil temperatures and the suggestion that woodlands pose a higher risk of parasite transmission because they are associated with longer cyst survival times. Alternatively, or in addition, it could be that faeces avoidance is more difficult in woodland where it becomes more cryptic among the leaf litter. In other habitats, faeces is more clearly visible and may be much easier to avoid. In contrast, the reduction in parasite infections when the troop repeatedly uses all habitats seems contradictory to the results seen in the woodland. However, this finding might further support the idea that parasite cysts are unable to survive in the more open desert landscape, and/or that baboons are better able to avoid contact with faeces in such areas.

Finally, I found that baboon troops were less likely to revisit areas if they had high levels of parasite infection with small amoeba (across all habitats) and *B. coli* (in woodland), in support of H3. These results support the finding that mandrills with higher parasite burdens showed evidence of avoiding site recursion and fidelity (Poirotte, 2017a). However, the reason for this observed behaviour is still unclear (Bicca-Marques & Calegaro-Marques, 2016; Charpentier & Kappeler, 2018). For example, parasite infection may change the host's behaviour through disease, with lethargy and reduced fitness as a consequence of infection (Beldomenico, 2010). This is illustrated by the observation that an increase in mandrill protozoan richness is also associated with changes in the daily path length of the troop (Brockmeyer et al., 2015). Previous, evidence of parasite avoidance behaviour in baboons has

been mixed. Sleeping sites are a key location for faecal build-up in primates (Freeland, 1980), and Hausfater & Meade (1982) suggested that baboons avoid site fidelity of sleeping sites for this reason. Yet Anderson & McGrew (1984) found no such pattern of avoidance behaviour in baboon troops and their sleeping cliffs. Interestingly, troop movement may be influenced by the leadership of key individuals, including in this population (King et al., 2008), and arguably the infection status of the whole troop may not be indicative of those that decide where the troop should forage. Klemme & Karvonen (2018) showed that in paired salmon their avoidance of parasites was more likely when a dominant individual showed avoidance behaviours. A further complication is the potential pathogenicity of the infections: Hart (1990) argues that avoidance behaviours will only occur if the parasites have a cost to the host, yet some of the parasites carried in this population may be commensals (see Chapter 2). This may help to explain why the observed pattern of woodland avoidance was stronger with *B. coli* infections (with known pathogenic effects) than for small or medium amoeba infections (which are categories that combine probable or known commensals with pathogenic species).

CHAPTER SIX

Exploring the association between social network position and gastrointestinal parasite infections in wild baboons

ABSTRACT

As parasite infections are mediated by contact with others, it is possible that an individual's social network position is associated with its gastrointestinal parasite infections. I explored this possibility in a wild chacma baboon population in central Namibia. I hypothesised that sociality would either (1) shape exposure to parasite transmission, (2) provide health benefits that would help individuals to resist infection, or (3) reflect conspecific avoidance behaviours following infection. I assessed two measures of social network position (strength; betweenness) in two types of network (grooming; proximity) for individuals in two troops over a 6-year period (2009-2015). No effect of social network position was found for any of the parasite species/categories tested (three with direct transmission, two with indirect transmission), nor with parasite richness. Overall, these results suggest that parasite infections are more strongly influenced by other sources of individual and environmental variation than by sociality.

INTRODUCTION

Group-living presents various benefits for individuals, such as safety from predators and the collective acquisition and defence of food resources (Krause & Ruxton, 2002). However, there are also trade-offs and costs to sociality. One of these costs comes from the fact that some infectious agents are transmitted through conspecific contact or the use of shared habitats (Anderson & May, 1979). Therefore, higher sociality has been predicted to increase parasite prevalence, intensity of infection, and diversity (Freeland, 1976; Møller et al., 1993). These predictions have been supported by studies which compare parasite infection across host species, showing that hosts with a gregarious lifestyle have higher parasite burdens and species richness than those with a solitary lifestyle in both mammals (Ezenwa, 2004a) and birds (Poulin, 1991; Tella, 2002). Furthermore, within social species, individuals do not interact randomly or uniformly with each other. As a result, there can be substantial individual-level variation in the risk of exposure to parasites. This heterogeneous behaviour within social groups may then determine the heterogeneous distribution of parasites within populations (Bansal et al., 2007; Poulin, 2007).

Quantifying the patterns of interaction between individuals within a social group can be done using social network analysis. The connections identified between individuals can then be used to assess the possible pathways by which transmission of infectious agents can occur

(Moore & Newman, 2000). Social networks can be determined through a variety of measures of social interaction, including spatial proximity and direct contact between individuals. Within these networks an individual's spatial position can similarly be quantified with a variety of different metrics that capture different aspects of its connectivity with other network members (Croft et al., 2008). Different network measures may represent different parasite transmission routes, while metrics of network position can represent exposure to those routes. The two together can therefore indicate those individuals most at risk of transmitting or being exposed to parasites. For instance, social network analysis can show whether an individual has fewer connections or whether they are well-connected and thus act as a possible 'super-spreader' – a main source of the transmission of infectious agents (Lloyd-Smith et al., 2005).

Previous research investigating the link between social network positions and individual infection risk from a variety of infectious agents is summarised in White et al. (2017). In this chapter, I focused specifically on the transmission of gastrointestinal parasites within social species. These parasites are expelled from the host in the faeces, and transmission typically occurs through direct contact of the host with faecal- (and hence parasite-) contaminated material in the environment. A variety of studies have assessed the evidence for the influence of social network position on gastrointestinal parasite transmission within both group-living species and during social contacts in solitary-living species. Their approaches and findings are summarised in Table 6.1. These studies show social network position can be associated with gastrointestinal parasite infection, however, such an association is contingent on the host, the parasite, the type of social network, and the metrics of social position that were tested.

Host species	Parasite type	Parasite metric	Network type	Social metric	Results	Ref
Primates						
Japanese macaques	H & P	Richness; P/A; abundance	Grooming	Strength given		[1]
				Strength received	**Single parasite abundance**	
				Centrality given		
				Centrality received		
Brown spider monkeys	H & P	Richness; abundance	50m chain	**Strength**	**Richness, Species abundance**	[2]
				Betweenees	**Richness, Species abundance**	
				Closeness	**Richness, Species abundance**	
				Indegree		
				Outdegree	**Richness, Species abundance**	
Yellow baboons	H	Abundance	Grooming	**Social status**		[3]
				Social connectedness to females		
				Social connectedness to males		
Others (group living)						
Giraffe	H	P/A	500m chain	Within-clique strength		[4]
				Between-clique strength		
				Overall tie strength		
				Betweenness		
Bumblebee	P	Intensity	Pairwise contact	Degree centrality		[5]
				Contact rate to infected		
				Proximity to infected		
Others (solitary contact)						
Belding's ground squirrels	P	Prevelence	Trapping contact	**Infected degree**		[6]
				Overall and precontact degree		
				Closeness		
				Betweenness		
Chipmunk	H	Prevalence	Trapping contact	Unweighted in-degree		[7]
				Mean weighted in-degree		
				In-edge diversity		
				Mean weighted degree		
				Unweighted degree		
				Edge diversity		
			Trapping contact,			
Bluetongue lizards	H	P/A	burrow locations	Overall strength		[8]
				Dispersers		

Table 6.1. Summary of recent research on the influence of social network position on gastrointestinal loads in primates, other group-living species, and through social contact in solitary species. Parasite type, H= helminths; P = Protozoa. Bold type indicates where a social metric had a statistically significant effect on parasite infections; the 'Results' column further specifies which metric/s of parasite infection (given several studies assessed multiple metrics) BOLD indicates significant results. [1] MacIntosh et al. 2012; [2] Rimbach et al. 2015; [3] Akinyi et al. 2019; [4] Vanderwaal et al. 2016; [5] Otterstatter & Thomson 2007; [6] VanderWaal et al. 2013; [7] Grear et al. 2013; [8] Fenner et al. 2011.

A key group where we may expect a link between sociality and infection risk are primates. Primates are highly social mammals that actively engage in behaviours that may expose them to parasite transmission, e.g. grooming and associating in close spatial proximity. Across species, meta-analyses of primate group size and parasite richness has produced mixed results. Nunn et al. (2003) found that group size was a predictor for parasite richness, until the analyses controlled for species phylogeny. Another comparative study found no association between the two (Vitone, 2004). However, in simulations of primate group size and parasite risk, the structure of the social group was important in determining whether parasites would transmit across large groups (Griffin & Nunn, 2012), highlighting the potential importance of the social network structure. Moreover, in species-specific studies, group size has been associated with infection risk, such as infection with microparasites in mangabeys (*Cercocebus albigena*: Freeland 1979) and macroparasites in baboons (*Papio anubis* and *Papio* sp.: McGrew et al. 1989). Similarly, in western lowland gorilla (*Gorilla gorilla*) populations that faced an Ebola outbreak, individuals living in groups had a much higher death rate due to the disease than solitary gorillas (Caillaud, 2006). Less work has been done on social network analysis and parasite loads, although the trend is changing: Puga-Gonzalez et al. (2019) reported that between 2000-2017 the number of publications featuring the term "social network primates" increased tenfold, although only a few of these focussed on infectious disease. Within primate species, only three studies to date have explored associations between gastrointestinal parasites and social network position: in Japanese macaques (*Macaca fuscata yaqui*; MacIntosh, 2012), brown spider monkeys (*Ateles hybridus*; Rimbach, 2015), and yellow baboons (*Papio cynocephalus*; Akinyi, 2019). All three studies reported an effect of social network position on parasite loads (see Table 6.1). Nevertheless, it is difficult to assess the consistency of these findings given the different methodological approaches involved.

There are three ways in which social network structure might be related to gastrointestinal parasite infection in primates. An individual's social network position might be associated with (1) its exposure to parasite infection, (2) its health and therefore its ability to resist infection, and (3) the extent to which it is avoided by other individuals once parasitised.

In the first case, an individual's social network position may influence its risk of exposure to parasite infection. Specifically, more social animals may be at greater risk of infection than less social animals from parasites transmitted through a faecal-oral route (Ezenwa, 2004a). There are two possible mechanisms (Anderson, 1979; Arneberg, 2002; Nunn, 2006). First,

more social animals spend more time in the company of others, and therefore in the company of others' faeces. For instance, if individuals tend to congregate in shady areas then those areas are likely to become contaminated through an accumulation of faecal material. More social animals may be more likely to spend time in these shady areas and pick-up the parasites from the contaminated ground, the cysts/eggs adhering to their hands and subsequently being ingested during feeding. Second, animals who more actively groom others may also be at higher risk of infection. This is because some parasites may be similarly transmitted when the groomer ingests the particles that they are picking off the groomee during grooming, when those particles might include parasite cysts/eggs from grooming around the anogenital region or if the groomee has recently lain down on contaminated ground. Such mechanisms may explain why female Japanese macaques occupying social network positions with higher centrality have higher *Oesophagostomum aculeatum* eggs in their faeces (MacIntosh, 2012).

In the second case, an individual's social network position can influence its health, which may affect its ability to manage infection. The structure of the network should ultimately reflect individual strategies to promote individual fitness, and this may be shaped through multiple routes (Krause et al., 2007; Sueur et al., 2011). In fact, increased sociality has been shown to be associated with increased fitness in a variety of species, including chacma baboons (*Papio ursinus*), where strong and stable bonds were associated with longer life spans among females (Silk et al., 2009). Although the mechanism that underpins such patterns are still unclear, it is possible that more social animals gain health benefits through having 'friends' that provide social support, including tolerance at shared feeding sites and support during aggressive interactions. For example, in Japanese macaques, individuals with a higher centrality and dominance status had lower glucocorticoids, indicating that socially supported individuals were less stressed (MacIntosh, 2012). If such social support allows individuals to maintain a higher nutritional status and/or reduces stress, it is possible that this improves immune function and may also allow such individuals to fight parasite infections more effectively. Another possible mechanism is the transmission of potentially beneficial microbes (Archie & Tung, 2015; Koch & Schmid-Hempel, 2011). Zaiss & Harris (2016) summarise the research on parasitic helminths and gastrointestinal bacteria, suggesting that the gut microbiome may protect against helminths or improve a host's fitness through other means. Previous research has found relationships between sociality and gut microbiome structure in primates: Tung et al. (2015) found that the grooming network position of yellow baboons influenced their gut microbiome communities, while Orkin et al. (2019) found that

microbial communities, and the beta diversity of microbiomes, were clustered around social groups of their host, white-faced capuchins (*Cebus capucinus imitator*). Sociality has similarly been associated with gut microbiome richness and community structure for chimpanzees (*Pan troglodytes*: Moeller et al. 2016). Primate sociality may therefore be important for the transmission of potentially beneficially microbiomes, and thus shape an individual's ability to fight parasite infection.

In the third case, the association between social network position and parasite infection may not be one of cause (as in the previous two cases) but of effect, as an individual's social network position may change as a result of its infection status (Rushmore et al., 2017). There are multiple ways in which parasites can shape associative behaviour between social host animals (e.g. mate choice, aggressiveness, activity levels, spatial distribution, and group formation: Poulin 2018). These may result in an infected individual becoming less central in its network as it is avoided by others to reduce their risk of exposure and/or it becomes less socially active due to lethargy. Or alternatively, it may prompt an individual to increase its centrality, as the parasite promotes its host's social contact rates. Previous evidence in primates is suggestive of the former pattern, indicative of avoidance or lethargy reducing interactions between individuals. In vervet monkeys (*Chlorocebus aethiops*) a deworming of all troop members altered the social network, resulting in an overall increase in nearest neighbour 'degree strength' (a measure of the number and quality of relationships individuals share with one another), indicating that individuals were more social with others when they were not parasitised (Chapman et al., 2016). This effect was not universal across the troop, however, with juveniles showing the strongest response to the changes in parasite prevalence (Chapman, 2016). Poirotte et al. (2017) similarly found that mandrills (*Mandrillus sphinx*) showed avoidance towards individuals infected by parasites; the time mandrills spent receiving grooming was lower when their protozoan richness was high, and after the removal of parasites in some individuals, the amount of grooming they received increased.

The aim of this chapter is to test the association between individual sociality and parasite infection in a wild primate population. Specifically, I explore the three potential associations between an individual's social network position and its parasite infection status described above, through the following three hypotheses. First, Hypothesis 1 (H1), that social network position dictates the exposure of an individual to parasites. I test two alternative possibilities: H1a, that individuals who are more active groomers to others are more likely to be exposed to directly-transmitted parasites through physical contact with individuals, and H1b, that

individuals more often in proximity to others are more likely to be exposed to directly-transmitted parasites through greater exposure to contaminated faecal material. As a control group, I assess the same relationships for indirectly transmitted parasites, where I would not expect to see a pattern (Côté & Poulin 1995). Second, Hypothesis 2 (H2), that social network position is associated with individual health, such that animals with better social connections are better able to manage infection from both directly and indirectly transmitted parasites. Third, Hypothesis 3 (H3), that individuals with higher loads of directly transmitted parasites, but not indirectly transmitted parasites, have weaker social connections due to conspecific avoidance behaviours.

METHODS

This study was carried out at Tsaobis Nature Park, Namibia, and focussed on two troops of wild chacma baboons over the period 2009-2015. The study period encompassed 7 field seasons ranging in length from 2-7 months. Troop members were individually recognisable and habituated, and individual age was either established at birth or taken from dental examination. Individual dominance ranks were calculated annually based on social interactions. Tsaobis is highly seasonal and to quantify this variation I used a remote sensing: normalized difference vegetation index (NDVI). This was calculated across three months to measure seasonal variation. For further details on the study site and study population, see Chapter four: methods.

To describe the social networks, behavioural data were collected on patterns of grooming and spatial proximity using a combination of focal follows (in which one 'focal' individual is followed and their behaviour recorded over time), instantaneous scans (in which the current behaviour of multiple individuals is collected), and *ad libitum* data collection (in which specific events or interactions are recorded as they are seen). Grooming data were recorded using *ad lib* observations and focal monitoring. I recorded the identity of interacting individuals, whether they were groomer or groomee, and the length of time the grooming bout occurred for. Data were collected across 2009-2015. However, in 2009-2013, focal and *ad lib* observations were collected for all individuals, whereas in 2014-2015 data were collected *ad lib* on all individuals and through a subset of focal individuals. Nevertheless, the two methods produce comparable social networks: grooming networks built through focal and *ad lib* observations were significantly correlated (Mantel tests, Baniel et al. *in review*). Focal observations lasted from between 15 minutes to one hour. The focalling of individuals

occurred in a semi-random manner across four daily time periods (0600-0900, 0900-1200, 1200-1500, 1500-1800 hours): once an individual had been sampled they were not sampled again until after three hours, in order to maximise the independence of observations. Despite groomees and groomers switching roles within a grooming bout, a new bout was only recorded when a grooming partner changed, the grooming bout ended, or the two grooming partners moved to another location.

Proximity data were recorded using continuous focal follows (2009-2013) or scans of focals (2014-2015). During the focal follows and scans, the nearest neighbour within a 5 metre radius of the focal individual was recorded. If there were no neighbours within 5 metres then they were recorded as alone. Focal follows lasted from between 15 minutes to one hour. As for the grooming networks, these data were collected across four daily time periods (0600-0900, 0900-1200, 1200-1500, 1500-1800 hours) and, once an individual had been sampled, they were not sampled again until after three hours. For the scan data collection, the focal individual was randomly chosen and not resampled for at least one hour after the last observation. Further details of individual proximity assessment are provided in Castles et al. (2014), and the full methods of the scan data collection are described in Carter et al. (2016).

Parasite infection status

Gastrointestinal parasite infections were assessed for five species or species groups: three microparasite species/categories, all of which exhibit direct transmission through an oral-faecal route: *Balantidium coli*; medium amoeba (including the potentially pathogenic *Entamoeba histolytica*); and small amoeba; and two macroparasite species, both of which exhibit indirect transmission via insect vectors: *Streptopharagus pigmentatus* and *Physaloptera caucasia*. Parasite infections were also assessed using parasite richness, which combined both microparasites and macroparasites, and ranged between 0-6 (where species categories, such as small amoeba, were treated as a single taxon). The infection status of an individual was derived from faecal samples taken at fortnightly intervals across the field season, collected across the day during behavioural observations. The faecal samples were collected and stored in 10% formalin and analysed using the modified formol-ether technique (Allen, 1970). Presence/absence was recorded for all parasites. In addition, the eggs per gram (EPG) of macroparasites and the quantitative score of microparasite infections were recorded (for details of the scoring system, see Chapter 4, Section *Analysing faecal samples for parasites*). In total, 1202 samples were collected over the period 2009-2015,

across a total of 132 individuals across all age-sex classes. The median number of samples collected per year was 159 (range 109-281). To test hypothesis H1 (H1a, H1b), I used the presence/absence (1/0) of parasite infection. To test H2 and H3, I quantified infection levels based on the parasite burden. Because the macroparasite EPG data were zero inflated in the latter, the macroparasite abundance analysis was limited solely to the EPG among infected animals. H2 was also tested using total parasite richness.

Social network position

To explore the three hypotheses (H1 – H3) two different social networks were used. For H1a, assessing whether the time an individual spends grooming others impacts its exposure to parasites, I constructed a 'grooming' social network determined through the amount of time an individual grooms each other member of the troop. For H1b, assessing whether the time individuals spent in the company of others was related to their infection status, I constructed a 'proximity' network on the basis of the amount of time an individual spends in the company of others as determined by the identity of the nearest neighbour within 5m. Hypotheses H2 and H3 were tested using both types of network because neither of these hypotheses specify which aspect of social behaviour (physical contact or spatial proximity) is likely to be most important. The connections in each network were weighted, with the weighting ranging from zero for individuals with no connections to any other individuals, up to one for individuals which are maximally connected to all other individuals.

For each of these two social networks, two different metrics of individual network position were calculated: 'degree strength' and 'betweenness', both of which are measures of centrality, the extent to which an individual is at the centre of the periphery of the network. The former is a measure of 'direct centrality', in that it reflects relationships with immediate social partners, while the latter is a measure of 'indirect centrality', in that it reflects wider connections through the social partners' social partners. The degree strength (hereafter 'strength') is the sum of the weighted connections each individual has with all the other individuals in the network. The higher the value the more and/or the stronger the connections that individual has. Betweenness is calculated as the number of shortest paths that connect an individual to the weighted network, with higher betweenness indicating greater connectivity to different parts of the network. Because I was primarily interested in who grooms who more actively (H1a), the grooming network was constructed using out-directed interactions (i.e. the grooming given by the focal to another individual) leading to

outgoing directed metrics. However, directionality was not important for proximity associations, so the proximity network was unidirectional. Ultimately, animals with higher strength have a greater number of and/or more intense connections across the troop network, while animals with a higher betweenness have more connections with individuals that are otherwise unconnected.

Grooming and proximity networks were calculated for each year and each troop. All metrics of centrality were z-score transformed within each year to standardise the data, making the metrics comparable across years to account for differences in troop demography. All social networks were constructed, and metrics of individual position calculated, using R v3.6.0 (R Core Team, 2019) with the iGraph package (Csardi & Nepusz, 2006).

Statistical analysis

The three hypotheses (H1a, H1b, H2, H3) were tested through an exploration of the relationship between parasite infection (the response variable) and social network position (the predictor), after controlling for other potentially confounding variables. The precise response variable, and the pattern of the relationship between that variable and the social network position, varied between the different hypotheses, as summarised in Table 6.2 and graphically plotted in Figure 6.1. In order to assess these relationships, I ran 11 models: five presence/absence models (one for each parasite), five parasite abundance/intensity models (one for each parasite), and one parasite richness model. The presence/absence models tested H1a and H1b; the abundance/intensity models tested H2 and H3, and the richness model provided a further test of H2. All statistical analyses were run using R v3.6.0 (R Core Team, 2019).

Hypotheses	Predictions	Response	Predictors	Models
H1a. Individuals who are more active groomers are more likely to be infected by directly-transmitted parasites (through ingestion of eggs/cysts from the coat of groomees)	Animals with stronger GROOMING connections are more likely to be infected by DIRECTLY transmitted parasites	Occurrence of directly transmitted parasites (Control: Indirectly transmitted parasite occurrence)	Grooming strength Grooming betweenness	Five presence/absence models (one for each parasite species)
H1b. Individuals who are more actively associated with others are more likely to be infected by directly-transmitted parasites (through ingestion of eggs/cysts from the faecal material of others)	Animals with stronger PROXIMITY connections are more likely to be infected by DIRECTLY transmitted parasites	Occurrence of directly transmitted parasites (Control: Indirectly transmitted parasite occurrence)	Proximity strength Proximity betweenness	Five presence/absence models (one for each parasite species)
H2. Individuals with better social connections are in better health and therefore better able to manage infection from both directly- and indirectly-transmitted parasites	Animals with stronger connections are less likely to be heavily infected by both DIRECTLY and INDIRECTLY transmitted parasites	Abundance of directly and indirectly transmitted parasites & Parasite richness	Grooming strength Grooming betweenness Proximity strength Proximity betweenness	Five abundance models (one for each parasite species) & One model for parasite richness
H3. Infected individuals are avoided by other conspecifics	Animals with heavier infections by DIRECTLY transmitted parasites are less likely to be strongly connected	Abundance of directly transmitted parasites (Control: Indirectly transmitted parasite occurrence)	Grooming strength Grooming betweenness Proximity strength Proximity betweenness	Five abundance models (one for each parasite species)

Table 6.2. Summary table of the hypotheses, their predictions, and how these were tested.

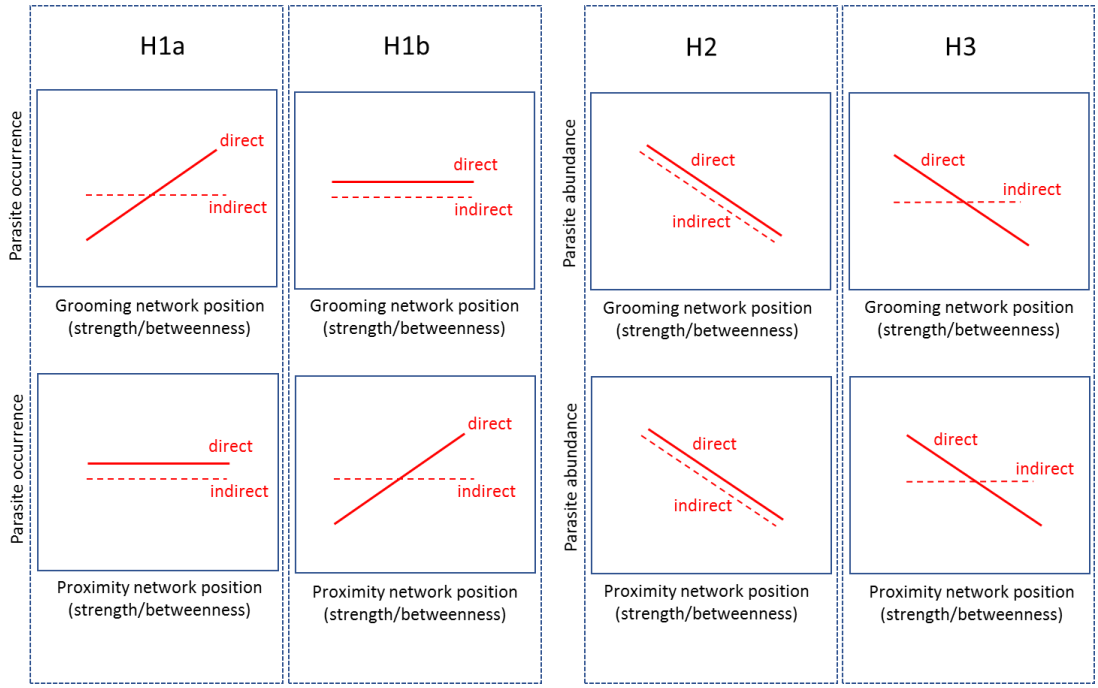


Figure 6.1. Graphical summary and comparison of the predicted relationships between social network position and parasite infection for both directly and indirectly transmitted parasites for each of the hypotheses under test.

I used generalised linear mixed models (GLMMs) and linear mixed models (LMMs), interpreted using AIC selection with the package 'lme4' (Bates, 2015). To test H1a and H1b, the presence/absence of each parasite was fitted using a binomial distribution. To test H2 and H3, the abundance score of each microparasite was fitted using a Poisson distribution, while the intensity of macroparasite infection (eggs per gram >0) was log transformed and fitted as a Gaussian distribution. In a further test of H2, richness was fitted as a Poisson distribution. The predictors in each model comprised the 'best fit' social network position metric of the four possible metrics (see below) plus the following control variables that may also influence an individual's exposure and susceptibility to parasite infection: age (as a polynomial), sex, troop, dominance rank, 3 months NDVI (as a measure of seasonal environmental variation) and 12 months NDVI (as a measure of interannual environmental variation). There was no evidence of collinearity between variables, tested using a Pearson correlation matrix, except between 3-months and 12-months NDVI which exceeded the standard $|r|>0.7$ threshold (Dormann, 2013). Therefore, the models only included 3-months NDVI. Interactions were also fitted between 3-months NDVI and the social network metric, to allow for the possibility that the effects of sociality on parasite infections may only be detectable in unusually wet or dry period. To manage potential pseudoreplication as a result of repeatedly sampling individuals, I also included baboon ID as a random effect. For the

abundance and intensity of parasites, the raw data were fitted and the mass of the faecal sample was included as a log offset.

In order to avoid the inclusion of four social network position metrics as predictors in a single model (grooming strength and betweenness, proximity strength and betweenness), or otherwise the quadrupling of the number of models required if each model only contained one of these four metrics, I ran some initial analyses to identify the 'best fit' social network position metric in each cases. This was achieved by running the above 'full' models (i.e., with all predictors present) for each of the four potential metrics, and comparing the AIC values between those four models. The model with the lowest AIC value was identified as the model containing the best fit social network position metric, and only that metric was then used in that analysis.

Once the best fit metric had been identified for each analysis, I used the information-theoretic approach for model selection in that analysis (Burnham, 2002). Thus I considered all possible combinations of fixed effects and compared the fit of each model through Akaike's information criterion (AICc), with the R package MuMIn (Barton, 2016). All models with less than Δ6 AIC units were selected. This was because AIC often selects unnecessarily complex models, so when simpler versions of these models with better AIC were also selected these were preferred (the nesting rule: Richards 2008; Arnold 2010). After the application of the nesting rule, if more than one model remained in the top set then model averaging was used to calculate the parameter estimates and standard errors of the final composite model. This final composite model was determined using the model.avg function in the MuMIn package with full-coefficient modelling. The effects of any variables in the model that had confidence intervals crossing zero were deemed to be inconclusive (du Prel, 2009).

RESULTS

The proximity and grooming networks differed substantially from one another in both troops L and J (Figure 6.2), highlighting that the position metrics derived from these different networks capture different aspects of the sociality of the individuals tested.

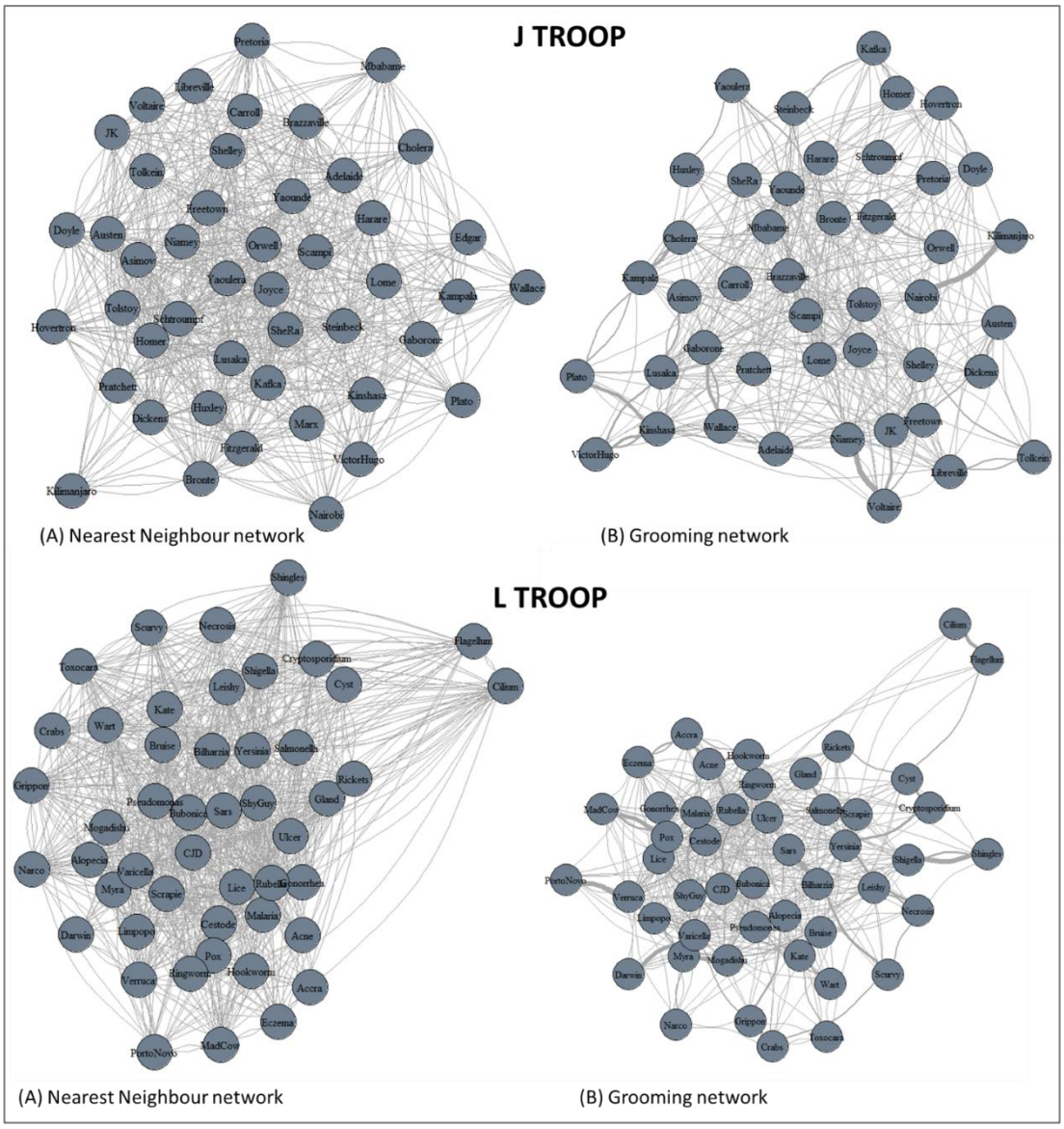


Figure 6.2. Social network plots illustrating the variation in an individual's network position between the (A) nearest neighbour (proximity) network with the (B) grooming network. Plots constructed from 2014 data.

Relationships between social network position on parasite presence / absence (H1a, H1b)

For all three microparasite models, grooming betweenness was the best fit social network position (with the lowest AIC). This suggests more support for the contact-mediated exposure of H1a than the proximity-mediated exposure of H1b. However, after model selection, grooming betweenness only appeared in the final model for medium amoeba, and in that model its confidence intervals crossed zero (Table 6.3, top section). There is therefore no support for either H1a or H1b. Nevertheless, parasite occurrence was predicted by other non-network predictors: 3-months NDVI had a consistent positive effect on the presence of

all three parasites. Age was also an important factor for medium and small amoeba, although showing a non-linear relationship with both, with reduced occurrences in younger and older animals (the coefficient of the 2nd-order polynomial term was conclusively non-zero in both cases). Additionally, sex and dominance rank were associated with medium amoeba, with females, and higher ranked individuals, more likely to be infected with medium amoeba.

Control analyses were also carried out for the two macroparasites' occurrence. In these cases, different best fit network metrics were obtained: proximity betweenness for *S. pigmentatus*, and grooming strength for *P. caucasia*. However, in neither case did these metrics enter the final models, and none of the other variables showed any conclusive associations (all confidence intervals crossed zero) (Table 6.3, bottom section).

Relationships between social network position and parasite abundance/intensity (H2, H3)

For the abundance of infection for all three microparasites, and *S. pigmentatus*, proximity betweenness was the best fit network metric. However, after model selection, proximity betweenness failed to enter any of the final models for microparasites, and although present was inconclusive in the final model for *S. pigmentatus*. For *P. caucasia* intensity, proximity strength was the best fit metric, and appeared in the final model, but again it showed no evidence of having any conclusive association (Table 6.4). These results fail so support either H2 or H3.

With respect to other non-network predictors of parasite burden, 3-months NDVI had a positive influence on abundance in all three microparasite models, but only conclusively associated with small amoeba and *B. coli*. Age was also associated with abundance in two cases, with a higher intensity of infection in early adulthood for small amoeba and in younger animals with medium amoeba. Finally, animals of higher dominance rank had lower infection burdens for medium amoeba. There were no variables that showed any strong association with the intensity of macroparasite infection in either species (Table 6.4).

Parasite	Analysis	Network	Parameter	Estimate	Standard Error	95% confidence intervals Lower	Upper
Presence / Absence Directly transmitted							
B. coli	Binomial	Grooming	Betweenness	**NDVI 3 months**	1.130	0.147	NA	NA
				Sex	-0.416	0.144	NA	NA
Small Amoeba	Binomial	Grooming	Betweenness	Dominance Rank	1.347	0.809	-0.879	2.713
				NDVI 3 months	2.273	0.233	1.818	2.729
				Age (poly 1)	143.232	11.769	120.16	166.298
				Age (poly 2)	-10.808	4.784	-20.185	-1.431
				Sex	1.639	0.803	-0.966	3.017
Medium Amoeba	Binomial	Grooming	Betweenness	**Dominance Rank**	-3.538	0.843	-5.190	-1.886
				Groom betweenness	-0.327	0.135	-0.613	0.038
				NDVI 3 months	1.134	0.258	0.629	1.640
				Age (poly 1)	99.429	14.188	71.621	127.238
				Age (poly 2)	-15.867	5.420	-26.490	-5.244
				Sex	3.524	0.815	1.927	5.122
Presence / Absence Indirectly transmitted							
S. pigmentatus	Binomial	Proximity	Betweenness	Dominance Rank	-1.144	0.453	-2.102	0.356
				Sex	-0.512	0.312	-0.481	0.342
P. caucasia	Binomial	Grooming	Strength	Groom strength	0.193	0.107	-0.122	0.373
				NDVI 3 months	-0.157	0.104	-0.307	0.126
				Age (poly 1)	10.578	4.836	-4.532	19.984
				Age (poly 2)	7.673	3.745	-3.555	14.763
				Troop	0.439	0.257	-0.294	0.420
				Sex	-0.422	0.278	-0.295	0.232

Table 6.3. Model coefficients, standard errors and 95% confidence intervals for mixed effects models. Summarising the variables that were selected in the final models, and their association with the parasite. Those in bold represent variables that have conclusive associations between the dependent variable and the predictor, either by model selection resulting in one model, or the coefficients do not cross zero. Reference values for category variables: Troop = L troop; Sex = Male.

Parasite	Analysis	Network		Parameter	Estimate	Standard Error	95% confidence intervals	
							Lower	Upper
Abundance								
Directly transmitted								
B. coli	Poisson	Proximity	Betweenness	**NDVI 3 months**	0.238	0.056	NA	NA
Small Amoeba	Poisson	Proximity	Betweenness	**NDVI 3 months**	0.331	0.057	NA	NA
				Age (poly 1)	4.432	1.057	NA	NA
				Age (poly 2)	-2.487	1.051	NA	NA
Medium Amoeba	Poisson	Proximity	Betweenness	**Dominance Rank**	-0.738	0.225	-1.179	-0.298
				NDVI 3 months	0.123	0.049	-0.011	0.227
				Age (poly 1)	0.952	0.843	-0.699	2.603
				Age (poly 2)	-2.840	0.816	-4.439	-1.242
				Sex	0.411	0.150	0.061	0.724
Intensity								
Indirectly transmitted								
S. pigmentatus	Gaussian	Proximity	Betweenness	Dominance Rank	-55.855	43.346	-140.812	29.102
(log +1)				NDVI 3 months	-6.057	10.138	-25.928	13.813
				Proximity betweenness	12.416	12.014	-11.131	35.963
				Age (poly 1)	213.880	162.267	-104.157	531.916
				Age (poly 2)	-110.314	152.692	-409.585	188.958
				Sex	21.414	28.437	-34.321	77.150
				Troop	10.832	23.392	-35.016	56.680
				NDVI:Proximity	8.547	15.114	-20.943	36.885
P. caucasia	Gaussian	Proximity	Strength	Dominance Rank	-2.329	2.094	-5.617	2.403
(log +1)				Proximity Strength	1.397	0.577	-0.102	2.609
				Age (poly 1)	3.863	7.591	-11.015	18.741
				Age (poly 2)	-0.283	6.948	-13.902	13.335
				Sex	-0.766	1.454	-2.855	1.891
				Troop	1.732	1.103	-1.011	3.728
				NDVI 3 months	-0.683	0.456	-0.701	0.492

Table 6.4. Model coefficients, standard errors and 95% confidence intervals for mixed effects models. Summarising the variables that were selected in the final models, and their association with the parasite. Those in bold represent variables that have conclusive associations between the dependent variable and the predictor, either by model selection resulting in one model, or the coefficients do not cross zero. Reference values for category variables: Troop = L troop; Sex = Male.

Relationships between social network position and parasite richness (H2)

For parasite richness, proximity strength was the best fit network metric. However, although present in the final model, its effects were inconclusive, failing to support H2 (Table 6.5). Although three other non-network predictors also entered the final model, namely NDVI, age, and sex, all were inconclusive with the exception of age: richness tended to increase in older animals.

						Standard	95% confidence intervals	
Parasite	Analysis	Network		Parameter	Estimate	Error	Lower	Upper
Richness	Poisson	Proximity	Strength	NDVI 3 months	0.034	0.177	-0.018	0.066
				Proximity strength	0.030	0.019	-0.025	0.046
				Age (poly 1)	1.829	0.671	0.401	3.187
				Age (poly 2)	-1.029	0.593	-2.193	0.175
				Sex	-0.065	0.040	-0.102	0.054

Table 6.5. Model coefficients, standard errors and 95% confidence intervals for mixed effects models. Summarising the variables that were selected in the final models, and their association with the parasite. Those in bold represent variables that have conclusive associations between the dependent variable and the predictor, either by model selection resulting in one model, or the coefficients do not cross zero. Reference values for category variables: Sex = Male.

Summary of social network trends

A summary of the predicted trend between social network position metric and parasite infection according to each hypothesis (see Table 6.2, Figure 6.1), and the results obtained, is provided in Table 6.6. These results show that, even in those four cases when the network metric entered the final model, its effect was not only inconclusive but consistently in the opposite direction to that predicted.

Hypothesis	Network type	Expected trend	Observed trend, according to parasite					
			B.c	SA	MA	*S.p*	*P.c*	PR
H1a	Grooming	+	0	0	–	/	/	/
H1b	Proximity	+	0	0	0	/	/	/
H2	Grooming	–	0	0	0	0	0	0
	Proximity	–	0	0	0	+	+	+
H3	Grooming	–	0	0	0	/	/	/
	Proximity	–	0	0	0	/	/	/

Table 6.6. Summary of the expected and observed trends between social network metrics and parasite infection. Key: + positive relationship; - negative relationship; 0 network metric does not enter final model; / no relationship predicted. *B.c* = *B. coli*, SA = small amoeba, MA = medium amoeba, *S.p* = *S. pigmentatus*, *P.c* = *P. caucasia*, PR = parasite richness.

DISCUSSION

In this study I tested three hypotheses about how the social network position of an individual might influence its parasite infection status. These hypotheses involved three different measures of infection status (parasite presence/absence, parasite abundance, and parasite richness) involving five different parasite species/categories, two different measures of social interaction (grooming networks and proximity networks), and two different metrics of individual position within these networks (strength and betweenness). Nevertheless, none of the hypotheses received any support, suggesting that there is no relationship between social network position and parasite infection in this baboon population. Instead, other aspects of individual variation, especially age, and environmental variation, namely vegetation greenness (NDVI) over the preceding 3 months, were the primary predictors of parasite infection. Such predictors appeared in the best models for both directly and indirectly transmitted parasites, but their effects were more conclusive for those parasites with direct transmission.

Despite the lack of any clear relationship between social network position and parasite infection, there were some intriguing patterns in the results. It was particularly notable that the best fitting network metrics were usually derived from the grooming network in the presence/absence models, but from the proximity network in the parasite abundance and richness models. This might be indicative of two different ways in which sociality may be shaping parasite transmission in individual baboons: that the actual transmission of parasites is driven through physical contact, but parasite burden following infection is driven by proximity, presumably through the sorts of mechanisms described by hypotheses H2 and H3. However, given that these metrics usually failed to enter the final models, and in those cases when they did their effects were inconclusive and in the opposite direction to that predicted, it seems perhaps more plausible that the consistency of grooming versus proximity effects in the different analyses may be coincidental.

These results contradict a recent study of baboon sociality and parasite infection. Akinyi et al. (2019) found that female grooming network position was associated with helminth infections: animals with greater connectedness had lower helminth richness and a lower abundance of *Trichuris trichiura*, but a greater abundance of *Physaloptera (Abbreviata*) *caucasia* (*caucasica*). The positive association with the indirectly transmitted *P. caucasia* was proposed to arise because better connected individuals were better able to access the best

food resources, in this case those invertebrates that acted as the parasite's vector. The network associations with *T. trichiura* and richness did not include the whole network; in the first case, *T. trichiura* egg output was specifically associated with the connectedness of adult females to adult males (with the opposite association found in Habig et al. 2019), and in the second case, adult female connectedness to other adult females was associated with lower helminth richness.

As in the example above, there are many alternative ways in which social networks have been created in order to explore transmission risk. Mostly, these explored the sex differences in network connections (see Akinyi, 2019; Habig, 2019) or explore other variables that are associated with social network positions (e.g. dominance rank; MacIntosh, 2012). Additionally, social networks may be biased towards related individuals, for example in Mandrills there is evidence that social affiliation is determined by maternal and paternal kin relationships (Charpentier, et al., 2007). In this study I included all associations between individuals of all ages, sexes, and kin relationships in the same network, and so were unable to disentangle any such associations involving sex-specific contacts or kin biased affiliations, and whilst the analysis in this study accounted for the effects of sex and age, it did not include relatedness. If social networks are shaped by kinship, underlying influences of genetic susceptibility may be overlooked. Indeed in other baboon species there is evidence of both maternal and paternal bias in affiliation (*P. cynocephalus*: Alberts et al., 2006; Silk et al., 2006; *Papio anubis*: Lynch et al., 2017). However, in this study population, there is evidence that grooming networks are not restricted to related individuals and proximity (as determined through co-feeding) are more strongly associated with grooming relationships than with kinship (King et al., 2011). Whether this remains the case when determining these relationships for female baboons only is unknown, with Silk et al. (2010) finding that females are more likely to form bonds with closely related, or similarly aged, females. Overall, further exploration into the factors that shape social network position and connectivity should be considered when determining their importance for disease transmission.

There are several possible reasons why I was unable to identify any conclusive associations between an individual's sociality and their parasite presence, richness, or abundance.

First, there may be multiple drivers shaping the association between social network position and parasite infection. If more central animals are more exposed to parasite transmission (H1), but also better able to resist infection due to the health benefits associated with

centrality (H2), it's possible that the combination of both effects leads to no observable pattern. A similar cancelling out might occur if both H1 and H3 were combined.

Second, I might fail to find a relationship between centrality and microparasite infections in the case of proximity measures because the proximity network is based on the identity of the nearest neighbour within 5m and this may not be the best way to identify individuals who spend a lot of time with other individuals. Proximity networks based on alternative measures, such as the identities of all neighbours within 10m, or the identities of all neighbours whose most peripheral member is within 5m of another individual of that neighbour group (see Carter et al. 2016, Figure 1), may be more effective.

Third, the networks constructed for the two baboon troops were constructed over yearly intervals, representing social interactions across three to six months per year. Yet dynamic social networks might be required in order to explore sociality and parasite transmission. Rushmore et al. (2013) illustrated that in great apes, social networks were variable across months, and suggest that dynamic networks may be more effective for assessing parasite transmission in primates. This is because dynamic networks incorporate the social changes that occur as a response to the environment or a disease outbreak (see also Farine 2017). Simulations of static versus dynamic social networks using *Cryptosporidium* sp. spread through Verreaux's sifakas (*Propithecus verreauxi*) found that outbreak predictions were very different between the two networks, with dynamic networks resulting in much larger outbreaks than those occurring in static networks (Springer et al., 2017). If avoidance behaviours are occurring across a shorter temporal resolution than studied here I may be missing some of the more nuanced social behaviours shaping parasite transmission.

Finally, it may be that identifying how social network position influences parasite infection is more challenging than might be expected. Simulations looking at the individual network centrality index found that the importance of sociality was reliant on the transmission probability of the parasite (Griffin, 2012). It seems likely that the probability of parasite transmission when baboons contact one another is variable, or low, meaning that we cannot easily capture the importance of social contact and proximity through social network metrics alone. Additionally, whilst an individual who is more central may be at higher risk of parasite transmission we may fail to capture this difference in risk by using static networks. In models of parasite spread through a simulated social network, infectious agents were transmitted faster for more central individuals, but infection soon spread to other individuals resulting in

a network where parasite distribution across the network was no different than the spread within a random network (Romano et al., 2016). Overall exploring the potential influence of social network position on patterns of infection by a particular parasite species may be difficult in wild populations.

CHAPTER SEVEN

Assessing the influence of inbreeding, immune gene diversity, and genotype-by-environment interactions on parasite infection on wild baboons

ABSTRACT

Inbreeding and low heterozygosity can make individuals more susceptible to parasite infection, especially under conditions of environmental stress. To investigate these patterns in a wild primate population I tested four hypotheses relating the severity of parasite infection to: inbreeding; immune gene diversity at the *Mhc-DRB* region of Major Histocompatibility Complex (MHC); the presence of a specific *Mhc-DRB* supertype; and the mediating role of the environment in a wild baboon population. I found that baboons were more likely to be heavily infected with *Physaloptera caucasia* if they were inbred, and more likely to have a higher parasite richness and to be infected with small amoeba if they had a low MHC allele richness. In addition, the effects of allele richness on parasite infections were mediated by the 'greenness' of the environment (assessed using a satellite measure), suggesting a G_H x P x E (host genome x parasite x environment) interaction. However, there was no effect of the tested *Mhc-DRB* supertype on parasite infections. These results suggest that both inbreeding and immune gene diversity in the host can influence the parasites it carries, the latter especially under certain environmental conditions.

INTRODUCTION

Individuals must survive and reproduce in environments comprising a multitude of abiotic and biotic factors all of which are changing or evolving. The ability of individuals to cope with such changes across space and time is strongly influenced by their genetic diversity, or 'heterozygosity'. High heterozygosity maintains adaptive capacity and reduces the probability of deleterious alleles being expressed (Reed & Frankham, 2003). This is especially true for the hosts of parasites and pathogens, which generally have shorter generation times and so can rapidly adapt to common genotypes, giving parasites an evolutionary advantage over their hosts (Clark, 1976; Jaenike, 1978). As a result, high host genetic diversity serves as a buffer to disease outbreaks (Altizer et al., 2003).

One way in which individuals maintain high heterozygosity is through the avoidance of breeding with related individuals, or 'inbreeding'. The offspring of inbreeding tend to have lower heterozygosity and are more likely to express recessive deleterious alleles, significantly affecting their survival, reproduction, disease susceptibility, and ability to respond to environmental stressors (Keller & Waller, 2002). Such impacts, which have also been shown to apply to parasite infections in a variety of taxa (Table 7.1), can in turn lead to 'inbreeding

depression' in the affected populations. The impact of inbreeding is sufficiently serious that a range of inbreeding-avoidance behaviours occur across taxa (Pusey, 1987; Waldman & McKinnon, 1993), including sex-biased dispersal, extra-group copulations, and the ability to recognise kin/familiar individuals and/or detect genetic similarity (see Pusey & Wolf 1996 for summary).

Species	Observed effect of inbreeding	Reference
California sea lions (*Zalophus californianus*)	The parental relatedness of individuals was an important factor in the susceptibility of individuals to infection by helminths.	Acevedo-Whitehouse et al. (2003)
Guppies (*Poecilia reticulata*)	Under different breeding regimes, individuals were shown to vary in susceptibility to ectoparasites, with inbred animals carrying a higher abundance of parasites and maintaining the infection for longer.	Smallbone et al. (2016)
Galápagos hawks (*Buteo galapagoensis*)	Inbreeding associated with higher abundance of ectoparasites.	Whiteman et al. (2006)
Bumblebees (*Bombus terrestris*)	Colonies with lower genetic diversity showed an increase to parasite susceptibility, including increase prevalence, increased intensity, and increased parasite species richness.	Liersch & Schmid-hempel (1998)
Soay sheep (*Ovis aries*)	Inbreeding associated with reduced survival due to increased susceptibility to parasitism.	Coltman et al. (1999)
Glanville fritillary butterfly (*Melitaea cinxia*)	Reduced heterozygosity led to an increase in the pupal period, increasing the risk of parasitism. Inbreeding also associated with local population extinction.	Saccheri et al. (1998)

Table 7.1. A selection of studies reporting the effects of inbreeding and lower genetic diversity on parasite infection.

One area in which high heterozygosity may be particularly important is in immune genes, such as the major histocompatibility complex (MHC). The MHC is an important part of the vertebrate immune system, enabling recognition of pathogens by producing molecules that bind to antigens of the parasite or pathogen initiating further immune responses. The diversity of MHC molecules increases the range of pathogens that they can respond to, as more alleles across multiple loci increases the diversity of pathogen-derived antigens that

can be recognised. As a result, higher heterozygosity of the MHC loci should enable a host to mount an immune response against a greater range of pathogens (Doherty & Zinkernagel, 1975). At the population-level, a higher MHC allelic diversity reduces the opportunities for a single pathogen to spread across the population and result in a disease outbreak (Hedrick & Kim, 2000). MHC genes are split into three subgroups: classes I, II, and III. MHC class II is important for studying gastrointestinal parasite infection as this class of genes is largely associated with extracellular pathogens (Jensen, 2007). MHC allelic richness has been found to covary with parasite occurrence in a number of species. In the hairy-footed gerbil (*Gerbillurus paeba*), a greater number of alleles was associated with lower nematode egg counts, but not parasite presence/absence (Harf & Sommer, 2005). In bank voles (*Myodes glareolus*) a polynomial relationship has been reported with those individuals carrying an intermediate number of alleles carrying the fewest nematode species (Kloch et al., 2010).

In addition to allelic richness, the presence of specific MHC genes may also be critical. For example, in house sparrows (*Passer domesticus*), two specific alleles were correlated to resistance to malaria (Bonneaud et al., 2006); in montane water voles (*Arivola scherman*), an association was found between a specific MHC allele and parasite infection (Tollenaere et al., 2008); and in giant pandas (*Ailuropoda melanoleuca*), a single MHC allele was associated with infection of one helminth species (Zhang et al., 2015). However, identifying such associations can be challenging. In systems where there are a high number of MHC alleles, testing the association of each allele with each parasite increases the probability of Type 1 errors, potentially generating spurious inferences of association. For instance, in banded mongooses (*Mungos mungo*), single-locus heterozygosity showed no significant associations with parasite abundance when type 1 errors (multiple testing) were accounted for (Mitchell et al., 2017).

It is also important to consider that while host susceptibility to infection is a product of the interaction between host and parasite genomes, the dynamics of these interactions can be shaped by the environment in which the host and parasites live, giving rise to G_H x P x E (host genome x parasite x environment) effects. These influences can occur at multiple points in the parasite infection cycle, either altering the host's susceptibility to infection, or the host's probability of host exposure to parasites (Hall & Ebert, 2012). For example, *Daphnia magna* living under experimental stressors showed G x P x E effects on both the ability of the parasite to establish itself within the host, and on the host's ability to clear infection when a parasite has established itself (Hall, 2012). Similarly, an association between MHC allele richness,

parasite infection, and host survival was found in three-spined sticklebacks (*Gasterosteus aculeatus*) experiencing environmental stress in the form of a heatwave (Wegner et al., 2008). Such effects are likely to reflect the fact that mounting an immune response is a costly process (Derting & Compton, 2003; Lochmiller & Deerenberg, 2000). In terms of environmental effects on exposure, infection rates are often acknowledged to be higher under certain environmental conditions. In primates, wet seasons are associated with higher infection rates, for instance howler monkeys (*Alouatta palliate*; Milton, 1996), chimpanzees (*Pan troglodytes* (Huffman et al., 1997), gorillas *Gorilla gorilla* (Watts, 1998), and baboons *Papio ursinus* (Benavides et al. 2012a). There are multiple reasons for these seasonal shifts: seasonality drives parasite survival, changes host behaviours, and alters food availability and thus host body condition.

Understanding the impacts of inbreeding, MHC genotype, and the role of the environment in mediating G_H x P interactions is becoming ever more important in recent years. This is because climate change, and habitat loss and fragmentation, are increasingly reducing population sizes and the connectivity of wild populations (Bijlsma & Loeschcke, 2012; Chapman, 2005; Epps et al., 2005; Hitchings & Beebee, 1998). Smaller populations are at greater risk both of losing heterozygosity through genetic drift and of higher levels of inbreeding (Cowlishaw & Dunbar, 2000; Frankham, 2003; Goossens et al., 2006). The deleterious effects of small population size are long-lasting: populations that have experienced historical bottlenecks carry their low genetic diversity into re-established populations. For example, wild populations of black howler monkeys (*Alouatta pigra*) were found to have lower genetic diversity than expected for their current population size, possibly due to a restricted population size in previous years (James et al., 1997).

Here I assess such inbreeding and MHC G_H x P x E effects in a wild primate population. I test four hypotheses. First, that more inbred individuals will have more severe parasite infections (hypothesis 1, H1). Second, that individuals with lower MHC allele richness will have more severe parasite infections (H2). Third, that the presence of specific MHC alleles affects individual parasite infections (H3). Fourth, that the environment may play a mediating role in the interaction between MHC richness and parasite infection, leading to G_H x P x E interactions (H4). I test these hypotheses in a wild population of chacma baboons (*Papio ursinus*) in Namibia.

Whilst baboons employ various strategies to avoid inbreeding, there is evidence that inbreeding occurs in wild populations, with inbred infants showing higher mortality than outbred infants (olive baboons, *P. anubis*: Packer 1979; yellow baboons, *P. cynocephalus*: Alberts & Altmann 1995). Generally, baboons predominantly adopt an inbreeding avoidance behaviour of sex-biased dispersal: males leave their natal troop once they reach sexual maturity to join an unrelated troop whilst the females remain philopatric. Male-biased dispersal helps to minimise inbreeding in baboons, although it does not prevent it entirely as natal males occasionally fail to disperse or engage in reproductive activity prior to leaving their troop (Alberts, 1995). If dispersal fails, or if mating occurs prior to dispersal, baboons are able to discriminate maternally related kin to avoid inbreeding (Alberts, 1995; Pusey, 1996). However, chacma baboon populations in Botswana where males failed to disperse from their natal troop, the survival or their offspring after 90 days did not differ from the offspring of males that had transferred into the troop (Bulger & Hamilton, 1988). Whilst Bulger & Hamilton (1988) hypothesise that the cost of inbreeding against the benefits of not dispersing from the troop has allowed this population to exhibit a more flexible approach to inbreeding avoidance, it does not explore the degree to which kin discrimination is implemented to avoid inbreeding with related natal members. Despite the fact that relatedness can be discriminated through olfactory cues, e.g. volatile compounds are more similar in more closely related baboons (Célérier et al., 2010) baboons are likely to determine paternal relatedness from social cues (Erhart et al., 1997), e.g. age (Alberts, 1999). This differs from other primate species, for example Mandrills (*M. sphinx*; Charpentier, Peignot, et al., 2007), where individuals are able to discriminate kin based on phenotypic cues (Charpentier et al., 2017). Furthermore, whilst other primate species, e.g. Mandrills, choose mates based on MHC dissimilarity (Setchell & Huchard, 2010), there is little evidence that chacma baboons (*P. ursinus*) discriminate mates to ensure MHC diversity (Huchard et al., 2010a). Whilst most studies have considered the fitness costs on inbreeding in baboons based on infant survival (Alberts, 1995; Bulger, 1988; Packer, 1979), but few studies consider the long-term consequences of inbreeding. Overall, previous evidence of inbreeding in baboon populations and the mixed evidence of fitness consequences make them an interesting species to study when considering the relationship between genetic diversity and parasite susceptibility.

The baboons in this population have been typed for their *Mhc-DRB* sequences of alleles, and on the basis of their physicochemical amino acid properties categorised into supertypes (Huchard et al., 2008). This allows me to assess both allele richness (for hypotheses H2, H4) and the effects of specific MHC genes (H3). In particular, one of these supertypes (S1) is

associated with lower body condition and smaller sexual swellings in oestrous females (Huchard et al., 2010b), so it is possible that the presence/absence of this supertype is associated with parasite presence/absence or abundance.

METHODS

This study was carried out at Tsaobis Nature Park, Namibia, and focussed on two troops of wild chacma baboons over the period 2005-2015. The study period encompassed 9 field seasons ranging in length from 2-7 months. Troop members were individually recognisable and habituated, and individual age was either established at birth or taken from dental examination. Tsaobis is highly seasonal and to quantify this variation I used a remote sensing: normalized difference vegetation index (NDVI). This was calculated across three months to measure seasonal variation. For further details on the study site and study population, see Chapter four: methods.

Assessing parasite infection status

I assessed three measures of the gastrointestinal parasite infections of 90 individual baboons, and how these change over time, through repeated faecal sampling and coproscopy. Samples were taken at fortnightly intervals across the field season, collected across the day during behavioural observations, and stored in 10% formalin. In total, 1428 samples were included in the analyses. They were then analysed using the modified formol-ether technique (Allen, 1970). For further details of sample collection and analysis, see Chapter four: methods. My first measure of individual infection status was the richness of parasite species obtained through a count of the total number of species (or species categories) present. My second and third measures were the presence/absence and intensity of infection, respectively, of the following five parasite species and species categories: *Streptopharagus pigmentatus*, *Physaloptera caucasia*, and *Balantidium coli,* as well as the Medium amoeba and Small amoeba categories. The parasites *Chilomastix mesnili* and *Toxocara* sp. were included in the richness data but not analysed as separate species due to their scarcity in the population. I used faecal egg counts and cyst abundance scores, above zero, to assess the intensity of infection within the host. In itself parasite egg/cyst abundance may not reflect the abundance of adult parasites within the host, but it does reflect the fecundity and fitness of the parasite (Gillespie, 2006). On this basis, egg/cyst abundance should be a relevant measure of infection with which to assess the efficacy of the host's immune response.

Assessing the degree of inbreeding

The degree of inbreeding in an individual is typically expressed as its inbreeding coefficient (*f*), ranging from 0 (completely outbred) to 1 (completely inbred). Inbreeding coefficients can be calculated in two ways: from pedigrees or from molecular marker data. Traditionally *f* was determined through multi-generational pedigrees, but this requires the observation of species across multiple generations (Balloux et al., 2004). In long-lived species, or species that partake in extra-pair or promiscusous mating, it can be difficult to obtain the necessary data to build the pedigree (Charpentier et al., 2007b). This can be particularly challenging when studying species such as primates. Consequently, I calculated inbreeding coefficients with neutral molecular markers, specifically microsatellite loci, using COANCESTRY (v1.0.1.7) software (Wang, 2011). Genotyping errors were accounted for using bootstrapping methods and the software calculated the 95% confidence intervals for each inbreeding estimate.

The microsatellite data required to calculate the inbreeding coefficients were previously generated and made available to me for this study. In brief, over the 2005-2015 study period, 135 individuals of known age that had been sampled for parasites were genotyped at 16 polymorphic microsatellite loci. These individuals were genotyped using nucleic DNA extracted from tissue samples or, for a small number of cases faecal samples, stored in 70% ethanol. The tissue samples were collected as ear biopsies during troop capture events whilst the individual was under anaesthesia. Capture events occurred in 2005, 2006, and 2012. The DNA was extracted using the Qiagen extraction kit and amplified via PCR. Genotyping across the 16 loci involved five different multiple-mixes, using fluorescent primers, on an AB1373/ABI377 sequencer. All individuals were genotyped at least twice, whilst homozygotes were genotyped a minimum of three times to avoid error occurring from allelic dropout. Allelic frequencies were analysed visually and using the software GeneMapper. A full description of the methods is available in Huchard, Knapp, et al. (2010).

Assessing MHC genotypes

The MHC genotype data required for this study were similarly previously generated and made available for this study. Of the 135 individuals identified above, 90 were also genotyped in the *Mhc-DRB* region of the MHC Class II genes. This region plays an important role in parasite resistance (reviewed in Huchard, Knapp, et al. 2010). Genotyping was carried out

with DNA from the same tissue samples used for the microsatellite loci (see above). Full details are provided in Huchard et al. (2006; 2008).

Across the population, 23 distinct *Mhc-DRB* sequences, hereafter 'alleles', were identified. Each individual carried between 2–8 of these different alleles (mean ± SD: 5.38 ± 1.60, n=199 individuals). However, in the dataset used in this study we there was one individual with 9 different alleles. These alleles were also classed into supertypes: groups of MHC alleles whose molecules overlap in their antigen-binding affinities and thus likely to share similar functionality. Across the population, 12 discrete Supertypes were identified. Each individual possessed 2-8 different supertypes (mean ± sd: 4.96 ± 1.47, n=199). For further details, see (Huchard, 2010a). Critically, Huchard et al. (2010) found an association between the presence of Supertype S1 with poor body condition and the poor expression of a sexual signal in females (smaller swelling size, and variation in swelling shape).

Statistical analysis

I initially analysed whether parasite infection status was affected by an individual's inbreeding coefficients (*f*) (hypothesis H1), its number of *Mhc-DRB* alleles (H2), or its possession of *Mhc-DRB* Supertype S1 (H3). I used generalized linear mixed models (GLMM) with parasite infection status as the response variable. Infection status was measured in three ways: parasite richness, parasite presence/absence (for five species/categories) and parasite abundance/intensity (for five species/categories), leading to a total of 11 models. Parasite intensity is the measure of abundance above 0. Three models, for parasite species richness, *Balantidium coli* and 'Medium amoeba' intensity, were fitted using the lme4 package (Bates, 2015) with a Poisson distribution. The abundance data for *S. pigmentatus* and *P. caucasia*, as well as for 'Small amoeba' were overdispersed (calculated using Harrison 2014), and therefore fitted using the glmmTMB package with a negative binomial distribution. Each presence/absence model, for *B. coli*, *S. pigmentatus*, *P. caucasia*, medium amoeba, and small amoeba, were fitted using the lme4 package (Bates, 2015) with a binomial distribution.

For all 11 models I incorporated the inbreeding coefficients, number of alleles and presence/absence of Supertype S1 as fixed effects. In addition, to test for the possibility of G_H x P x E effects (hypothesis H4), I included an interaction between the number of alleles and the total NDVI across the three months prior to sample collection. To account for

additional individual-level factors that may affect infection status (see Benavides et al. 2012), I also included sex, troop, and age (in a polynomial distribution) as fixed effects. Random effects included individual baboon identity, to control for the repeated sampling of parasite data from the same individual, and year. Additionally, I incorporated an offset of the log of the faecal sample mass, as the probability and number of parasites detected is likely to increase with faecal sample size. Collinearity between variables was tested using a Pearson correlation matrix, and no a correlation coefficient exceeded the standard $|r|>0.7$ threshold (Dormann, 2013). A summary of the models is presented in Table 7.2.

Response variables	**Data, distribution**
Richness	0-6 range, Log-transform Gaussian
Streptopharagus pigmentatus	Abundance, zero-inflated negative binomial
Physaloptera caucasia	Abundance, zero-inflated negative binomial
Balantidium coli	0-4 Score, Poisson
Medium amoeba	0-6 Score, Poisson
Small amoeba	0-6 Score, zero-inflated negative binomial
Fixed effects	
Inbreeding coefficient (*f*)	Range: 0 - 0.5
Number of alleles	Range: 2.0 - 9.0
Number of alleles : NDVI	Interaction with total 3 months NDVI
Supertype (S1) presence	Binomial
Troop	Two troops: 'L' and 'J'
Sex	Male and female
Age	Days old, polynomial
Random effects	
Individual baboon	90 individuals

Table 7.2. Summary of the response variables, fixed effects and random effects of the 11 models run.

I used model selection to establish which group of variables best explained the response variable. This was done by comparing the fit of each model through Akaike's information criterion adjusted for small sample size (AICc), with the R package MuMIn (Barton, 2016). AICc was used instead of AIC, as the sample size is small in comparison to the number of estimated parameters (Burnham, 2002). All models within Δ6 AIC units of the model with the lowest AIC were selected. I then used the 'nesting rule' to exclude those models that were more complex versions of nested (simpler) models in this set with better AICc support. This was because AIC often selects unnecessarily complex models, and simpler versions of the models with better AIC were preferred over more complex models (the nesting rule: Richards

2008; Arnold 2010). After application of the nesting rule, if more than one model remained in the top set then model averaging was used to calculate the parameter estimates and standard errors of a final composite model. This final composite model was determined using the model.avg function in the MuMIn package with full-coefficient modelling. Any variables that had confidence intervals crossing zero were deemed inconclusive (du Prel, 2009). All statistical analyses were conducted in R version 3.6.0 (R Core Team, 2019).

RESULTS

Of the 90 baboons contributing to this analysis, 43 were male and 47 female, with 34 from L troop, 53 from J troop, and three that transferred between both troops. The youngest was 28 days old, the oldest almost 25 years old (9,086 days old). Most were sampled multiple times, resulting in a total of 1,428 faecal samples. The median number of samples per individual was 15 (range 1-58).

The inbreeding coefficients ranged from $f = 0$ (n = 7) to $f = 0.505$ (n = 1), with a mean $f = 0.037$ ± 0.009 SEM (Figure 7.1). The mean MHC-DRB allele richness was 5.2 ± 0.17 SEM, and the prevalence of the S1 MHC Supertype was 48% (n=43/90).

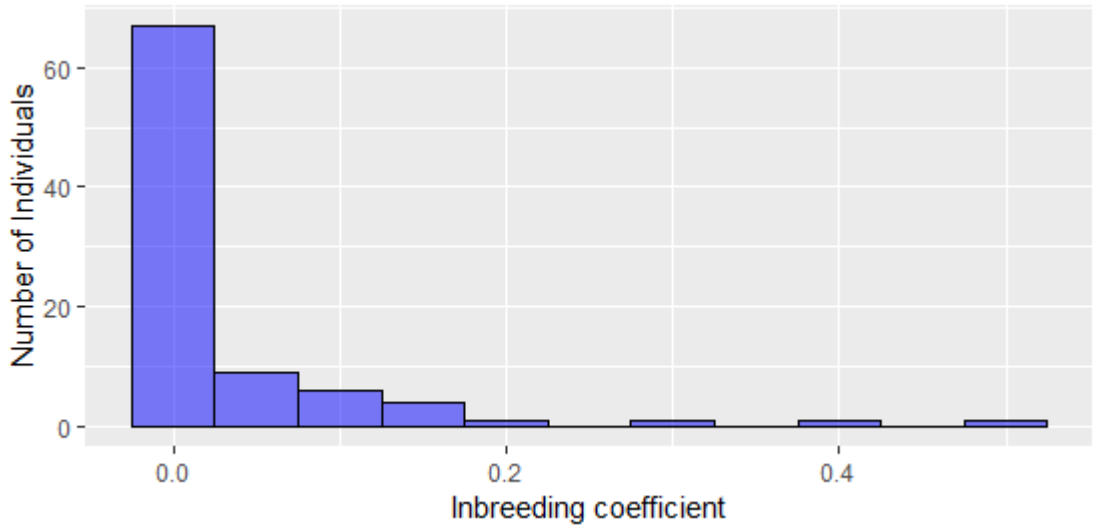


Figure 7.1. Frequency distribution inbreeding coefficients in the Tsaobis baboon population.

Several associations were identified between the host infection status, inbreeding coefficient, and MHC genotype (allele richness) (Table 7.3). In the case of H1, high levels of inbreeding were associated with a higher abundance of *P. caucasia,* in support of this

hypothesis, illustrated in Figure 7.2. However, no other conclusive effects of inbreeding were obtained. In the case of H2, high *Mhc-DRB* allele richness was associated with lower levels of parasite richness, and a lower likelihood of infection with small amoebae, in support of this hypothesis. However, no other conclusive effects of allele richness were obtained. In the case of H3, there was no evidence that the presence of Supertype S1 influenced parasite infection, contrary to this hypothesis. Indeed, the presence of S1 failed to appear in any of the best models. Finally, in the case of H4, wherever an effect of *Mhc-DRB* allele richness on parasite infection occurred, namely on parasite richness and the presence/absence of small amoeba, these effects were always mediated by the greenness of the environment over the preceding three months (3 month NDVI scores), in support of this hypothesis. The precise pattern of this interaction for parasite richness is illustrated in Figure 7.3, and for small amoeba in Figure 7.4. In the first case, baboons with higher allele richness have lower parasite richness during greener periods, but allele richness has minimal influence in drier periods, when parasite richness is consistently high. In the second case, baboons with higher allele richness are less likely to be infected by small amoeba during greener periods.

Surprisingly, four of the five abundance models failed to identify any consistent predictors, and in three of these four cases the null model provided the best model fit. Across all 11 models, only two other predictors were conclusively identified, the abundance of *P. caucasia* differed between troops (higher in J troop), and the incidence of medium amoeba differed between sexes (higher in females).

Parasite		Analysis	Parameter	Estimate	Standard error	95% confidence intervals	
						Lower	Upper
Richness	(log+1)	Gaussian	**MHC alleles**	-0.001	0.007	NA	NA
			MHC alleles : NDVI	-0.161	0.003	NA	NA
S. pigmentatus	P/A	Binomial	MHC alleles	0.003	0.061	-0.089	0.093
			MHC alleles : NDVI	-0.050	0.023	-0.089	0.030
	Intensity	Negative Binomial	Null model only			NA	NA
P. caucasia	P/A	Binomial	Troop	0.471	0.197	-0.096	0.884
	Intensity	Negative Binomial	**Inbreeding (*f*)**	0.179	0.067	0.003	0.325
			Troop	0.449	0.150	0.155	0.743
B. coli	P/A	Binomial	Inbreeding (*f*)	-0.155	0.065	-0.198	0.081
	Intensity (log+1)	Gaussian	Null model only			NA	NA
Medium Amoeba	P/A	Binomial (cloglog)	Age (polynomial 1)	-5.270	0.002	-8.341	1.549
			Age (polynomial 2)	-0.808	0.002	-1.278	0.237
			Sex	0.879	0.010	0.860	0.897
	Intensity	Negative Binomial	MHC alleles	0.012	0.011	-0.129	0.031
			MHC alleles : NDVI	0.013	0.006	-0.005	0.025
			Troop	0.072	0.039	-0.044	0.140
Small Amoeba	P/A	Binomial (cloglog)	**MHC alleles**	-0.109	0.002	NA	NA
			MHC alleles : NDVI	-0.243	0.002	NA	NA
	Intensity (log+1)	Gaussian	Null model only			NA	NA

Table 7.3. Model coefficients, standard errors and 95% confidence intervals for mixed effects models. P/A indicates the models for the presence or absence of parasites. Summarising the variables that were selected in the final models, and their association with the parasite. Those in bold represent variables that have conclusive associations between the dependent variable and the predictor, either by model selection resulting in one model, or the coefficients do not cross zero. Reference values for category variables: Troop = L troop; Sex = Male.

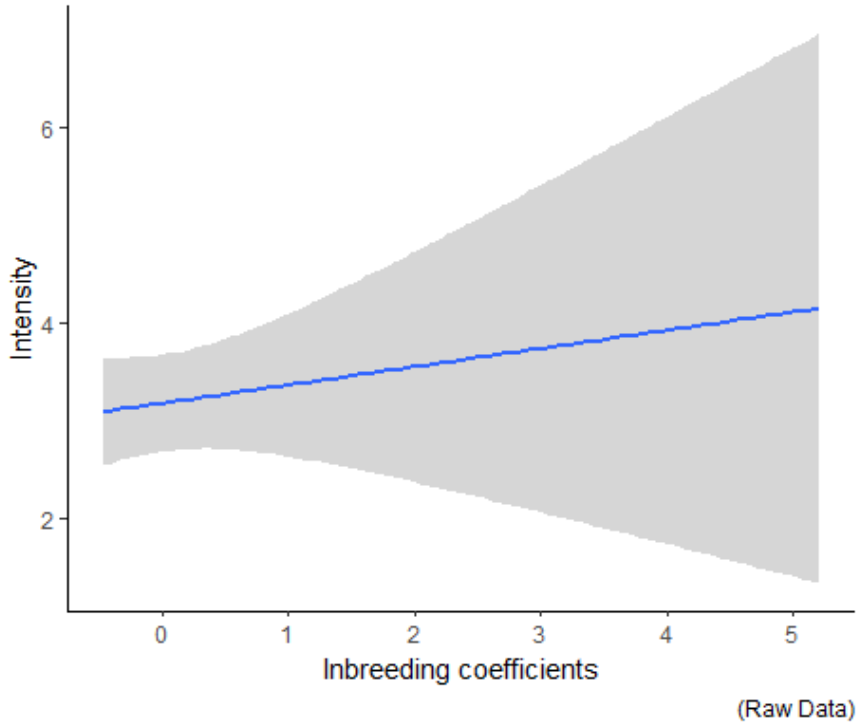


Figure 7.2. Relationship between intensity of *Physaloptera caucasia* with the inbreeding coefficients (*f*).

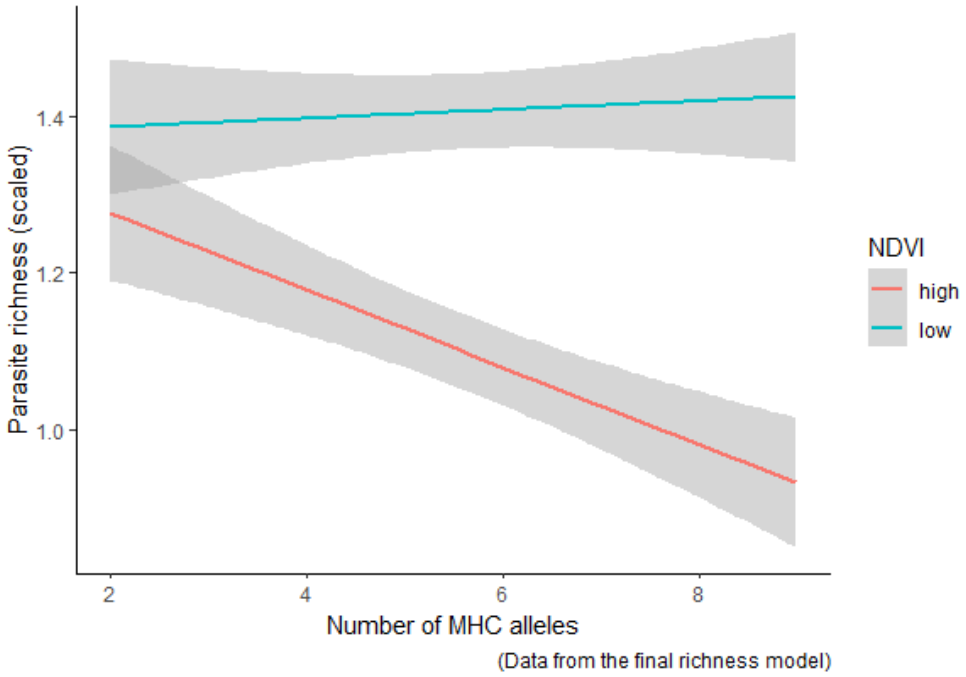


Figure 7.3. Relationship between parasite richness, *Mhc-DRB* allele richness, and greenness of the environment in the preceding 3-month period (3 month NDVI).

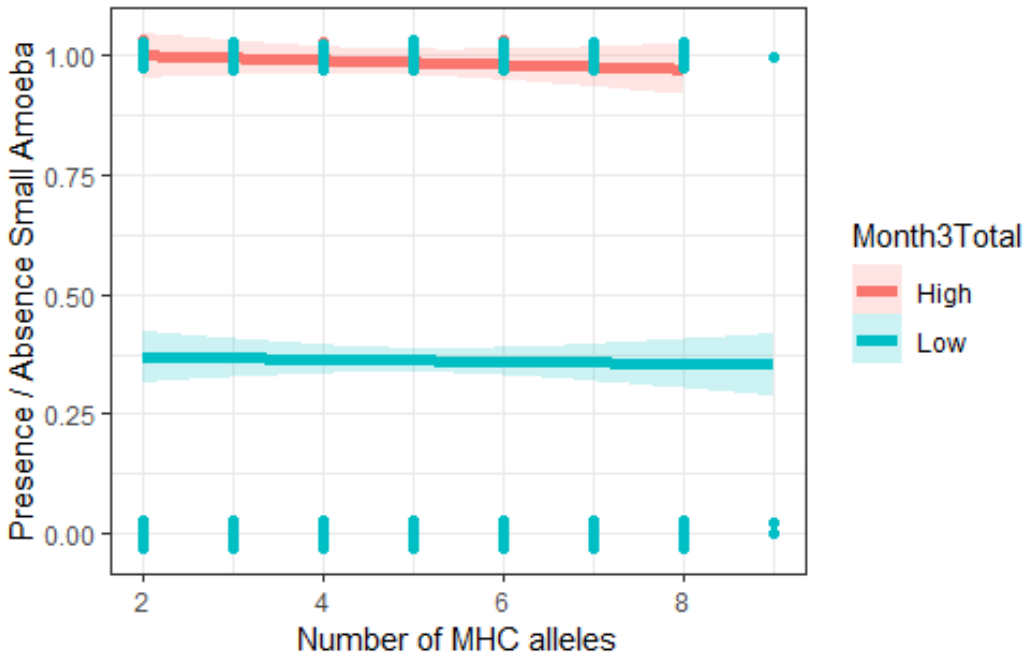


Figure 7.4. Relationship between small amoeba presence/absence, *Mhc-DRB* allele richness, and greenness of the environment in the preceding 3-month period (3 month NDVI).

DISCUSSION

This study tested four hypotheses about how parasite infections might be related to inbreeding, *Mhc-DRB* allelic richness, and specific MHC genes, in two troops from the Tsaobis baboon population. I also assessed the possibility that the effects of allelic richness might be mediated by environmental conditions in G_H x P x E interactions. I found evidence of some association between both inbreeding coefficients and the number of MHC alleles on some measures of parasite infection, in support of H1 and H2, and in some cases these effects involved an interaction with environmental factors (cumulative NDVI scores), in support of H4. However, there was no association between the presence/absence of specific MHC genes tested and parasite infection, contrary to H3. Interestingly, when testing for collinearity using Pearson's correlation, the inbreeding coefficients were not strongly correlated to *Mhc-DRB* allele richness (|r|= -0.27). This suggests that the effects of inbreeding were not mediated through an effect on *Mhc-DRB* allele richness, and that *Mhc-DRB* allele richness is largely independent of the current levels of inbreeding in this population. This is evident in the populations of other species, with inbreeding impacting neutral marker heterogeneity, but other selective pressures maintaining MHC diversity, likely due to pathogen-mediated selection (Spurgin & Richardson, 2010). For example, in Arctic fox (*Vulpes lagopus*) and in San

Nicolas Inland fox populations (*Urocyon littoralis dickey*) that had been through a genetic bottleneck, individuals maintained their MHC heterogeneity despite the homozygosity of the neutral markers (Aguilar et al., 2004; Ploshnitsa et al., 2012). Additionally, these differences are illustrated in the association between neutral marker heterogeneity and MHC diversity in their ability to predict population viability (Manlik et al., 2019). However, despite the inbreeding coefficients not correlating to MHC allelic richness, there were significant relationships between these two parameters with host susceptibility to parasite infection.

Inbreeding and parasite infections (H1)

The inbreeding coefficients (*f*) of the baboons included in this analysis ranged from 0 - 0.5. The mean *f* = 0.037 and 92% of individuals had an inbreeding coefficient > 0 (n = 83/90). Close inbreeding (*f* ≥ 0.25) was observed in 3% of individuals (n=3), and moderate inbreeding (0.25< *f* >0.125) observed in 6% of individuals (n=5), following the criteria for close and moderate inbreeding described by Nichols (2017).This degree of homozygosity is not uncommon in other wild animal populations. For instance, banded mongoose populations have 14% moderately inbred and 8% closely inbred (Nichols et al., 2014). A summary of other populations with individuals showing >0.25 inbreeding coefficients is presented in Keller & Waller (2002; Table 7.1). However, there is little evidence of inbreeding coefficients being greater than 0.25 in other primate species. Inbreeding coefficients of mandrills (*Mandrillus sphinx*) ranged between 0.00-0.25 (Charpentier et al., 2006). In hamadryas baboons (*Papio hamadryas*), no individuals had inbreeding coefficients above 0.25, however the average *f* for males was 0.12 and for females was 0.09 (Baume & Lapin, 1983). This indicates that overall the average inbreeding in the Tsaobis populations is comparable to others despite a few individuals being closely inbred.

In support of H1, more inbred individuals exhibited a higher output of *Physaloptera caucasia* eggs, suggesting that inbreeding can be detrimental in this system and impair the ability of baboon hosts to fight infections with this parasite. Surprisingly, the same pattern was not seen for parasitic amoeba or for parasite richness overall. Nevertheless, in California sea lions, helminths were similarly the parasite types more likely to be associated with inbreeding depression (Acevedo-Whitehouse, 2003). This conflicts with a meta-analysis reporting that heterogeneity was more important for determining susceptibility to microparasite infections, rather than macroparasite infections, however, ectoparasites were included in the analysis

(Ekroth et al., 2019). Why inbreeding might be more detrimental for resisting helminth infections than for amoebic infections, and then only certain helminths (there was no comparable effect on *S. pigmentatus* infections), remains uncertain.

In this analysis, *f* was calculated using neutral markers, which estimates inbreeding through similarities in the nucleotide sequences between individuals, i.e. through identity-by-state (IBS). Prior to this study, an attempt was made to calculate inbreeding coefficients by constructing a pedigree, which would have allowed inbreeding to be estimated through identity-by-descent (IBD), but this was unsuccessful due to shallow pedigree depth (Cowlishaw, personal communication). It is unclear whether different results might have been obtained with pedigree-based inbreeding coefficients. Both methods, pedigree and neutral markers, should generate inbreeding coefficients that reflect IBD heterozygosity. In fact, pedigree-derived inbreeding coefficients are based on the expected heterozygosity while molecular marker-derived coefficients are based on the observed heterozygosity and may therefore be a more accurate measure. However, whilst the use of molecular markers and heterozygosity may be expected to produce a closer representation of inbreeding, pedigrees are thought to capture ancestral genetic information and detect inbreeding from previous generations, while a large number of genetic markers are required to accurately estimate inbreeding (Slate et al., 2004). Ultimately, pedigree-derived inbreeding coefficients do appear to differ from the genetically-derived inbreeding coefficients: individual-based simulations have determined that the results from these two methods only weakly correlate with each other (Balloux, 2004). Despite this, using neutral markers should have successfully captured the fitness costs of inbreeding: not only do they capture Mendelian segregation (Forstmeier et al., 2012), they also represent the actual genomic heterozygosity. In contrast, as explained by Charpentier et al. (2007), being able to determine pedigrees in primates is difficult as their long generation times make it challenging to accumulate sufficient data to calculate inbreeding coefficients.

Mhc-DRB alleles and G x E x P interactions (H2-4)

Greater *Mhc-DRB* allelic richness was associated with lower parasite richness and a lower likelihood of infection with small amoeba, in support of H2. The question remains why these patterns were not observed for other parasitic amoeba or helminths. In this analysis, I hypothesised a negative linear relationship between MHC allelic richness and parasite egg output. This is evidenced in the association between MHC diversity and the diversity of

pathogen recognition (Penn et al., 2002). However, theoretical models have predicted that MHC alleles are subjected to two opposing selective forces through the process of positive and negative selection of T-cells (De Boer & Perelson, 1993; Nowak et al., 1992). The negative selection of T-cells ensures a reduction in their autoreactivity, and the greater the diversity of MHC alleles the more opportunity for self-reactivity, which results in a reduction in T-cell diversity for pathogen identification. The resultant optimal diversity of MHC genes is, therefore, at an intermediate threshold (Nowak, 1992), and thus we should expect to see a quadratic polynomial relationship between MHC richness and parasite richness. This relationship has been apparent in other species e.g. in experimentally inbred three-spined stickleback (*Gasterosteus aculeatus*; Wegner et al., 2003), and in bank voles (*Myodes glareolus*; Kloch et al., 2010) the relationship between parasite richness and MHC allele diversity fits the optimality hypothesis. Nevertheless, even when considering the linear relationship between MHC allelic richness and parasite richness or parasite presence / absence, a significant association was found.

In addition, both of these patterns involved interaction effects with environmental conditions (NDVI), in which the patterns of infection were high and independent of allele richness during drier conditions, but where patterns of infection declined with higher allele richness in wetter conditions. One possible explanation for this pattern might be that, when animals are in poor condition, during dry periods, they are limited in their ability to mount an immune response to parasites irrespective of their allele richness; but when in good condition, in wet periods, they can mount an effective immune response provided they have the appropriate *Mhc-DRB* alleles, which is likely to be a function of their allele richness. In support of this explanation, body condition improves in the Tsaobis baboons in wetter periods, including when those periods are measured by NDVI greenness (Cowlishaw, personal communication, unpublished results). These findings suggest there is some evidence for G_H x E x P interactions driving the dynamics of infection, at least for some parasites, in this system. This in itself is significant, given there is little evidence of G_H x E x P in other wild mammal (or even vertebrate) populations, and even G x E effects are difficult to uncover (Wolinska & King, 2009).

In contrast, there was no evidence of an effect of Supertype S1 on parasite infection, contrary to H3. The most likely reason I failed to find an effect is that any analysis of specific gene function needs to find the relevant genes to test, and this particular supertype may not have been the most relevant. It was selected because previous research had found it to be associated with lower body condition (Huchard, 2010b), and body condition is often associated with parasite abundance (Beldomenico et al., 2008), including in the Tsaobis

baboon population where animals in poorer condition exhibit higher parasite richness (Benavides et al. 2012a). However, the direction of the relationship between supertype S1 and body condition was in the opposite direction to that predicted if S1 played a role in the immune response to parasites: individuals who had this supertype were in poorer condition rather than better condition. Therefore, it is perhaps unsurprising that there was no association between S1 and parasite infection. Additionally, single alleles are considered important for each specific parasite species (Nowak, 1992; Wegner, 2003), and so the diversity or supertypes may only illustrate an individual's susceptibility to a range of parasite species (richness). Further research into single alleles and their association to parasite species is difficult, mostly as the statistical association may be prone to Type I error (e.g. Mitchell et al., 2017).

Overall, I found some evidence that genetic diversity plays a role in the susceptibility of an individual to parasite infection. Interestingly, the importance of MHC allelic richness was most notable under favourable environmental conditions. However, the association between genetic diversity and susceptibility was not consistent across all parasite species and further exploration into non-linear relationships between MHC allelic richness and parasite richness may illustrate an evolutionary advantage to optimising the diversity of immunity genes.

CHAPTER EIGHT

Discussion

OVERVIEW OF STUDY

The overall aim of this thesis was to explore the determinants of parasitic infections in wild baboons. Looking across continental-wide baboon-parasite associations, I found that parasite communities generally did not differ across different *Papio* species (excluding *P. hamadryas*), but were instead more likely to vary in association with environmental variables (see *Chapter three*). Within the Tsaobis baboon population, I found that host movement behaviour was associated with parasite infections. The repeated movement of troops into shaded habitats, i.e. habitats where parasite survival is higher, subsequently led to a higher prevalence of directly-transmitted parasite infection (see *Chapter five*). Additionally, baboon troops exhibited evidence of avoidance behaviour of high-risk habitats when parasite infection burden of directly-transmitted parasites was high (see *Chapter five*). Within troops, I found that individual social network position was not associated with parasite infection (see *Chapter six*), but that inbreeding and MHC diversity were associated with increased infections for some parasite species (see *Chapter seven*). Overall, this body of work shows a clear signal of environmental factors, mediated by individual host-level characteristics, both behavioural (movement patterns) and genetic (inbreeding, MHC allele richness), driving infection risk in this system. As such, we may predict that anthropogenic environmental change could dramatically alter future patterns and levels of parasitism in this system, and potentially altering human risk for parasites of zoonotic concern.

In this Discussion I will further synthesise my findings across chapters and their implications. Specifically, I will briefly review my findings for the effects of the three host traits on parasite infection (age, sex, rank) that were included as 'control' variables in my analyses of ranging behaviour, social networks, and genotype (*Chapters five*, *six*, and *seven*, respectively). I will then go on to consider environmental effects on parasite infection, a theme which similarly run through all three chapters, and attempt to reconcile my contrasting findings for avoidance behaviours (in *Chapters five* and *six*). Finally, I will briefly review our need to understand host-parasite dynamics in primates in response to habitat disturbance, and the importance of considering the conservation of parasites as well as their hosts in the future.

EFFECTS OF THREE HOST TRAITS ON PARASITE INFECTION

Host traits, such as age, sex, and social rank are important when considering an individual's risk to parasitism (Anderson, 1979; Nunn, 2006a). In *Chapter two* I reviewed the current consensus for which host traits were associated with parasitism in baboons, finding that: host age was correlated with parasite richness and abundance in a polynomial relationship; that sex differences are not apparent in parasite species richness, although some parasite species appeared to differ between sex; and that dominance rank was not associated with parasite richness. As a result of this, these three attributes were included as 'control' variables while analysing other determinants of individual variation in parasite infection status in the other chapters of this thesis: age (*Chapters five*, *six*, and *seven*); sex (*Chapters five, six,* and *seven*); and dominance rank (*Chapter six*). Here I summarise my findings across these chapters:

Age

Benavides et al. (2012b) previously reported a polynomial relationship between age and parasite richness, with younger and older animals carrying fewer species, in the Tsaobis baboon population between 2005-2006. Similar findings have been noted in other baboon populations. Pettifer (1984), for instance, observed the same pattern in parasite richness and age. However, when exploring age associations with the abundance of specific parasite species, many studies have reported more variable patterns that depend on the species in question (Akinyi, 2017; Meade, 1984; Müller-Graf, 1996). In this thesis, parasite species richness, as well as the presence/absence and abundance of individual parasite species, were analysed, with different chapters analysing different subsets of the Tsaobis baboon parasite data. In *Chapter five*, examining the spatial heterogeneity of infection risk, the polynomial distribution of age was positively associated with small amoeba presence, suggesting infections accumulated as hosts aged. However, no conclusive associations with age were found between medium amoeba, *B. coli*, *S. pigmentatus*, or *P. caucasia*. In *Chapter six*, examining social correlates of infection risk, parasite richness was positively associated with age, and the presence of small amoeba and medium amoeba was associated with the polynomial distribution of age. Additionally, abundance of small amoeba was associated with age in a polynomial relationship, whereas the abundance of medium amoeba was negatively associated with age. In *Chapter seven*, examining inbreeding effects, there were no associations between parasite species presence or incidence and individual age. Overall then, I found no consistent relationship between age and parasite richness, presence/absence, or

abundance, although small amoeba presence/absence and abundance were associated with age in two chapters. These results suggest that although some parasites may accumulate in hosts as they age (driving a broad positive association between age and infections), this tends to be a weak or non-apparent relationship, which may either be negated by (for example) increased acquired immunity as the host ages (potentially driving a polynomial age-abundance relationship; Cattadori et al. 2005; Woolhouse 1998), or be swamped by other factors (such as strong environmental drivers of infection in different age classes).

Sex

In a previous study of parasitic infections in the Tsaobis baboons, Benavides et al (2012) found that parasite richness was higher in females than males. I similarly found that females were more likely to carry medium amoeba, and to do so at high abundances, than males in all three chapters that analysed individual host traits (*Chapters five, six,* and *seven*). Such female-biased parasitism contrasts with the more typically observed male-biased infections seen in host-parasite systems (Moore & Wilson, 2002). This male-biased pattern is often attributed to the immune-suppressive effects of reproduction (Zuk, 1996), but it is unclear why the reverse pattern should be seen in baboons. Physiologically, reproductive costs may be reducing the ability for females to mount an effective immune response (Nordling et al., 1998). Otherwise females may show different behaviours to males which makes them more prone to parasite exposure (Meade, 1984). However, this female bias only seems to occur with medium amoeba: no other parasite species, or parasite species richness, showed any conclusive sex differences in this study. Furthermore, while these results support the findings of Benavides et al (2012), they differ from other publications of parasites in other baboon populations, where no differences between male and female parasites (Ryan et al. 2012; Ravasi 2009) or parasite species abundance (Meade 1984; Müller-Graf et al. 1996; Pettifer 1984) have been found. As with age, it is possible that sex-specific differences in exposure or susceptibility are swamped by stronger, possibly environmentally-related determinants of infection risk in this system. However, as we see consistent associations with medium amoeba and sex, but not other parasite species, it would be worth exploring behavioural differences between male and female baboons that may be altering their exposure to transmission.

Social rank

Previous analysis of the relationship between social status and parasite species richness failed to find an effect in the Tsaobis baboons (Benavides et al. 2012). In *Chapter six*, I found that higher ranking individuals were less likely to carry medium amoeba, and to do so at lower abundance, but otherwise there was no further evidence of an association between social rank and infection occurrence for any other parasite. Overall this lack of a relationship with social rank at Tsaobis aligns with other baboon studies that have similarly failed to find evidence of parasite infections being associated with dominance (Ravasi 2009; Benavides et al. 2012; Müller-Graf et al. 1996). In other primates though, some evidence of a relationship has been found. For example, in female Japanese macaques (*Macaca fuscata yakui*), an association between dominance and parasite infection was reported, with higher ranking individuals having a more parasite species and a higher number of *Oesophagostomum aculeatum* egg released in the faeces (MacIntosh, 2012). These associations were not mediated by social stress, as cortisol was lowest in high ranking individuals, and instead were suggest to be associated with sociality (MacIntosh, 2012). These results contrast the expectation that a higher rank confers a fitness benefit, as their position may allow for better access to resources, and instead suggests that dominance increases social contact. Since we found no association between baboon rank and sociality, or sociality with parasite risk, we would not expect to replicate the associations seen in Japanese macaques.

EFFECTS OF THE ENVIRONMENT ON PARASITE INFECTION

Appleton & Brain (1995), similarly observing a baboon-parasite system in the Namib Desert (in the Kuiseb population), suggested that parasites in semi-arid environments are more likely to be transmitted by social contact as their eggs and cysts would find it difficult to survive such a harsh environment. Tsaobis, along with Kuiseb, is hotter and drier than most of the other baboon sites studied and has a parasite community that reflects this (see *Chapter three*). Parasites that are common at other study sites, for example *Trichuris* sp. and *Ascaris* sp., are not present. These species are soil-transmitted, and as such may be limited by the environmental conditions present at the Tsaobis. The presence of the parasites that persist at Tsaobis suggests that they are either hardier, and therefore more able to avoid desiccation and persist under varying conditions, or are able to transmit with limited exposure to the environment, for instance through social networks and through intermediate hosts or

mechanical vectors. However, as described above, when exploring the influence of social network position on parasite infection no association was found (*Chapter six*), which would suggest that an ability to cope with extreme environmental conditions is the more likely mechanism. My finding that the recursive movement of troops predicts future patterns of parasite infection (*Chapter five*) further suggests that the parasites in the system are most likely transmitted via the environment, despite the environmental conditions apparently being too challenging for other parasite species.

In addition, seasonality has been associated with the fluctuations of parasite species richness in the Tsaobis baboon population (Benavides et al. 2012). Parasite richness covaried with temperature and increased after rainfall events (Benavides et al. 2012). While these results conflicted with some other findings of seasonality and baboon parasite infection in the literature (*Chapter two*). Other baboon habitats found that rainfall decreases the helminth infection (Akinyi, 2017; Pettifer, 1984), a pattern that is seen in other primates (*Mandrillus sphinx*; Poirotte et al., 2016). It is quite possible that this reflects the differences in environmental conditions between Tsaobis and other study sites, for example, I considered the rate of faecal degradation in a semi-arid environment (*Appendix six*) and found that, in contrast to other study sites, faeces remain present in the environment for long-periods of time and rainfall is not significant enough to disperse the faecal matter. Alternatively, these associations may be due to changes in parasite survival at different times of the season or reflect changes in host behaviour in response to the changes in their habitats. I explored seasonal fluctuations through monthly 'greenness' (NDVI) in the analyses. NDVI was both negatively (*Chapter five*) and positively (*Chapter six*) associated with medium amoeba and small amoeba presence. In *Chapter seven* the environmental conditions facilitate the impact of genetic diversity, with MHC allelic richness reducing parasite richness and small amoeba presence when there is higher NDVI 'greenness'. These also illustrate that the environmental conditions may be directly impacting the host's ability to mount an immune response, and thus change their susceptibility to infection.

RECONCILING THE PRESENCE AND ABSENCE OF AVOIDANCE BEHAVIOURS

In this thesis I looked at whether baboons avoided returning to heavily parasitised areas (*Chapter five*) as well as whether they avoided conspecifics who were heavily infected with parasites (*Chapter six*). In the first case, I found that troops were less likely to revisit areas when their burdens of *B. coli* and small amoeba were higher, suggesting a possible avoidance of high-infection risk areas. The avoidance behaviour of the Tsaobis baboon population was consistent across seasons, which differs from primates living in different habitats (e.g. Freeland, 1980; Poirotte, Benhamou, et al., 2017) where recursive behaviour increased after rainfall events, most likely due to rainfall dispersing the faeces and infectious agents from the environment. This is not the case at this study site, however, with rainfall causing no changes to the presence of faeces (*Appendix six*). In the second case, I found no evidence that individuals with a higher parasite output were shunned by their conspecifics leading to a reduction in their connections within a social network. Evidence from other studies suggests that individuals can use olfactory cues to assess the infection status of other individuals, e.g. in mandrills (*Mandrillus sphinx*: Poirotte et al., 2017) and in mongooses (*Mungos mungo*: Mitchell et al. 2017). However, this response has not been tested in baboons, and in other primates there is little evidence that avoidance is shown towards individuals with high levels of parasite infection (MacIntosh, 2012). Overall, whilst avoidance behaviours remain an important tool for many mammals to avoid infection (Hart & Hart, 2018), these behaviours come at a cost. The avoidance of grooming infected individuals could be detrimental to the baboon's access the resources and social tolerance (King, 2011; Sick et al., 2014), or could reduce the benefits provided from social interactions (Silk, 2006, 2009, 2010) that would ultimately decrease the susceptibility of the baboon to infection.

To further investigate whether we should expect baboons to show specific avoidance behaviours, it would be worth exploring which parasite species have a significant impact on host fitness. Avoidance behaviours are only likely to be evident when parasites incur some cost, and there is thus a benefit to behaviours that reduce exposure (Hart, 1990). As reviewed in *Chapter three*, many of the parasites in this baboon population are commensals. Many of the *Entamoeba* species, and *C. mesnili* show no evidence of being pathogenic to their host, and *B. coli* do not often harm their host. Similarly, the two helminth parasites in this population, *Physaloptera caucasia* and *Streptopharagus pigmentatus,* have relatively unknown life histories and pathogenicities. However, whilst these species may not be directly

pathogenic, they may still shape their host's fitness. In the Amboseli baboons, females with higher parasite species richness have longer interbirth intervals (Akinyi, 2019). Additionally, in rhesus macaques (*Macaca mulatta*), infection with *B. coli* has been associated with changes in milk composition suggesting possible consequences for offspring survival (Hinde, 2007). Further research into the costs these parasites incur is necessary in order to fully assess the cost-benefit trade-offs that parasite avoidance represents.

EFFECTS OF HABITAT DISTURBANCE ON PRIMATE PARASITE INFECTIONS

Changes in home range, and thus ranging behaviours, as a result of human landscape modification has been shown to impact pathogens, including gastrointestinal parasites (see Brearley et al. 2013 for review). For example, red-tailed guenons (*Cercopithecus ascanius*) living in logged areas, which reduces their natural habitat and restricts their home range, had higher levels of parasite infection (Gillespie, 2005). Additionally, there were higher levels of infectious parasites within the soil compared to those in non-human altered environments (Gillespie, 2005). Furthermore, in Tana River red colobus (*Procolobus rufomitratus*) and mangabey (*Cercocebus galeritus galeritus*) populations living in fragmented forests, parasite prevalence and richness were increased due to the increase in host density in these habitats (Mbora & McPeek, 2009). However, two species of howler monkeys (*Alouatta palliata Mexicana* and *Alouatta pigra*) across natural and fragmented habitats only showed a slight increase in parasite prevalence and richness (Trejo-Macías et al., 2007). The impact of these environmental changes are likely more important for terrestrial species rather than arboreal species (Mbora, 2009). As resources and habitats become more restricted it alters ranging behaviour, resulting in greater home range overlap and intensely used ranges, promoting increased exposure to parasites. A further impact from these changes is that a reduction in food availability from a changing habitat can reduce the host's body condition, and therefore reduce the host's ability to remove infection. In this thesis I have illustrated the importance of environmental factors in shaping parasite risk (*Chapters three, five, six, seven*) and the importance of spatial heterogeneity in shaping parasite transmission (*Chapter five*) in a terrestrial primate. Alterations to the habitat availability, through anthropogenic change, could have strong implications for the host-parasite interactions in this system. The Tsaobis baboons showed avoidance of repeatedly visiting habitats that pose a risk of parasite transmission (*Chapter five*) and restriction to their home ranges would limit their ability to

mitigate against parasite exposure. Furthermore, changes in the habitat conditions are likely to alter parasite survival, as I found that habitats with high levels of vegetation corresponded to higher parasite transmission. I also found evidence that NDVI interacts with the host's susceptibility to infection, possibly being associated with the effectiveness of mounting an immune response against parasites (*Chapter seven*). Changes in NDVI in this habitat may have profound effects on the susceptibility of a host to infection. Understanding the behaviour and ecological drivers of how resources and habitats shape parasite exposure should help conservation planning and our ability to accurately forecast the future spread of infection.

COINFECTION AND MICROBIOMES

Throughout this thesis, I have considered the dynamics of parasite richness and each parasite species individually. There is a wealth of evidence that parasites sharing a host have the potential to interact within the host, and considering parasites species in isolation may limit our understanding of the abiotic and biotic factors that shape a host's susceptibility to parasites (Johnson et al., 2015b; Telfer et al., 2010). However, if coinfection dynamics were playing a role in this system then it might be expected that as the abundance of one parasite species changes, another parasite species would consistently be presenting a change in abundance as a consequence of this. Throughout this thesis, parasite species have generally responded differently to different parameters, which is not to say that coinfection dynamics are not occurring, but that, as it stands, this research was unable to identify any associations between parasite species. When assessing the association of social network position and parasite infection (*Chapter six*), one of the hypotheses considered the importance the microbiome played in influencing the parasite communities within the host (Zaiss, 2016). Since the microbiome communities of primates, including baboons, is associated with social network connectivity (Archie, 2015; Goodfellow et al., 2019; Moeller, 2016; Orkin, 2019; Tung, 2015) it was expected that an association between social network position and parasite infection may be reflective of the host's internal microbiome. However, since no relationship was found between social network position and parasite infection, there was no evidence of interactions between the microbiome and parasite species.

BEYOND THE HOST: WHY PARASITE CONSERVATION MATTERS

Much of the research I have produced here has focused on baboon parasites not only for the purpose of understanding disease ecology generally but also with the view that we may use this knowledge to predict and navigate emerging infectious diseases. Undoubtedly this is a topic of concern to humans. Parasites are a threat to plant and animal populations, facilitating the extinction of species (Boots & Sasaki, 2002), economic losses (Gallup & Sachs, 2000), and impacting human health (Kuris, 2012). Yet, rather than justify the study of parasites on the basis of their impacts on human or charismatic host species, there are good reasons why parasites are important in their own right (Carlson et al., 2017; Dougherty et al., 2016). Any host-specific parasite is reliant on its host, and if that host goes extinct then so too will the parasite (Durden & Keirans, 1996; Gompper & Williams, 1998). Whilst we lack accurate numbers of parasites (Dobson et al., 2008; Poulin, 1996a) they might make up the majority of living species in the world (Windsor, 1998). Furthermore, they play an important role in maintaining the health of the ecosystem by controlling host populations and maintaining host genetic diversity (Windsor, 1995). Further, they are suggested to make up 75% of food webs (Dobson, 2008). With all this in mind, it is clear that parasites are an integral component of biodiversity. Their absence from an ecosystem would have large ramifications, possibly resulting in extinctions both locally and globally (Durden, 1996; Windsor, 1995). Consequently, keeping biodiverse communities intact should include preserving parasites within the ecosystem (Altizer, 2003; Gómez & Nichols, 2013). Ultimately, the biodiversity of parasite species should be welcomed and acknowledged, not just to predict disease outbreaks, but for a better understanding of the diversity of life (Brooks & Hoberg, 2000).

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APPENDIX ONE

SUPPLEMENTARY INFORMATION: CHAPTER THREE

Model selection

Table S3.1

Intercept	NDVI	Seasonality	Temperature	df	logLik	AICc	delta	weight
1.733	0.1021	0.08701		4	0.465	8.2	0	0.59
1.733	0.08066			3	-1.823	10.3	2.1	0.207
1.733			0.06445	3	-2.525	11.7	3.5	0.102
1.733				2	-3.709	11.7	3.53	0.101

Table S3.1. Final model selections of parasite species richness and environmental variables

Table S3.2

Intercept	Altitude	NDVI	Seasonality	Temperature	df	logLik	AICc	delta	weight
-0.2197	-3.92	1.338	-2.418	-3.089	5	-15.233	42.8	0	0.454
-0.1024	-2		-1.167	-1.334	4	-17.162	43.8	1.03	0.271
-0.02821	-0.8458				2	-19.979	44.4	1.6	0.204
0					1	-22.181	46.5	3.72	0.071

Table S3.2. Final model selections of presence / absence *Oesophagostamum* sp. and environmental variables

Table S3.3

(A)

Intercept	NDVI	Seasonality	df	logLik	AICc	delta	weight
-0.02334	-0.9548	0.6795	3	-17.58	42	0	0.424
0.0001365	-1.055		2	-18.84	42.1	0.08	0.408
0.009978		0.7993	2	-20.05	44.5	2.48	0.123
0			1	-22.18	46.5	4.47	0.045

(B)

Intercept	Rainfall	Seasonality	df	logLik	AICc	delta	weight
2.784	-0.03234	0.7544	3	-16.54	39.9	0	0.526
2.945	-0.03429		2	-17.99	40.4	0.45	0.42
0.009978		0.7993	2	-20.05	44.5	4.57	0.054

Table S3.3. Final model selections of presence / absence *Streptopharagus* sp. and environmental variables, with (A) model with NDVI and (B) with Rainfall.

Table S3.4

Intercept	Altitude	NDVI	Rainfall	Seasonality	df	logLik	AICc	delta	weight
1.186				1.084	2	-12.818	30.2	0	0.285
1.106	-0.945				2	-12.92	30.4	0.2	0.258
1.139		-0.98			2	-13.167	30.9	0.7	0.201
3.145			-0.0212		2	-13.604	31.8	1.57	0.13
0.9445					1	-14.824	31.8	1.64	0.126

Table S3.4. Final model selections of presence / absence *Physaloptera* sp. and environmental variables.

Table S3.5

Intercept	Latitude	Seasonality	df	logLik	AICc	delta	weight
-5.708	-1.202	-5.257	3	-5.618	18.4	0	0.605
-3.143		-2.821	2	-7.36	19.3	0.86	0.395

Table S3.5. Final model selections of presence / absence *Giardia* sp. and environmental variables.

APPENDIX TWO

SUPPLEMENTARY INFORMATION: CHAPTER FIVE

Table S5.1

Year												
						2005						
Month	Jan	Feb	Mar	Apr	May	**Jun**	**Jul**	**Aug**	**Sep**	**Oct***	**Nov**	Dec
GPS						**X**	**X**	**X**	**X**	**X**	**X**	X
Poop						X	X	X	X	X	X	X
Year							2006					
Month	Jan	Feb	Mar	Apr	May	**Jun‡**	**Jul‡**	**Aug**	**Sep**	**Oct‡**	**Nov**	Dec
GPS						**X**	**X**	**X**	**X**	**X**	**X**	
Poop					X	X	X	X	X	X		
Year							2009					
Month	Jan	Feb	Mar	Apr	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	Nov	Dec
GPS					**X**	**X**	**X**	**X**	**X**	**X**	X	
Poop							X	X	X	X		
Year							2010					
Month	Jan	Feb	Mar	Apr	**May**	**Jun**	**Jul**	**Aug**	Sep	Oct	Nov	Dec
GPS					**X**	**X**	**X**	**X**	X			
Poop					X	X	X	X				
Year							2011					
Month	Jan	Feb	Mar	Apr	May	**Jun**	**Jul***	**Aug**	Sep	Oct	Nov	Dec
GPS						**X**	**X**	**X**				
Poop						X	X	X				
Year							2012					
Month	Jan	Feb	Mar	Apr	**May**	Jun	Jul	**Aug**	**Sep**	Oct	Nov	Dec
GPS					**X**	X	X	**X**	**X**	X		
Poop					X	X	X	X	X	X		
Year							2013					
Month	Jan	Feb	Mar	Apr	**May**	**Jun**	Jul	**Aug**	**Sep**	**Oct**	Nov	Dec
GPS					**X**	**X**	X	**X**	**X**	**X**		
Poop					X							
Year							2014					
Month	Jan	Feb	Mar	Apr	**May**	**Jun**	**Jul***	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
GPS				X	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**
Poop									X	X	X	X
Year							2015					
Month	Jan	Feb	Mar	Apr	**May**	**Jun***	**Jul**	**Aug**	**Sep**	Oct	Nov	Dec
GPS	X			X	**X**	**X**	**X**	**X**	**X**			
Poop	X				X	X	X	X	X			

Table S5.1: Sampling months and years for GPS data collection and faecal sample collection. The bold x indicates that there are >300 GPS points in that month, and therefore the overlap data of these months is used, whereas too few data were collected in the months not highlighted in bold. *Indicates where the <300 data applies only to J troop, and ǂ indicates where the <300 data applies only to L troop.

Table S5.2

Intercept	NDVI	Small Amoeba	Troop	Year	df	logLik	AICc	delta	weight
0.1675	-0.0492	-0.06572	+	-0.03591	6	-77.848	167.8	0	1

Table S5.2: Final nested AICc model selection for the GLM of avoidance behaviour across all habitats. Summary of results in Table 5.2.

Table S5.3

Intercept	*B. coli*	Medium Amoeba	NDVI	Small Amoeba	Troop	Year	df	logLik	AICc	delta	weight
283.9	-0.0967	-0.07378	-0.2759	0.09146	+	-0.1407	8	-1477.74	2971.6	0	0.668
279.9	-0.1206		-0.2771	0.0802	+	-0.1387	7	-1480.03	2974.2	2.55	0.187
265	-0.0773	-0.06065	-0.2899		+	-0.1313	7	-1481.05	2976.2	4.59	0.067
279.5		-0.1045	-0.2741	0.0701	+	-0.1385	7	-1481.6	2977.3	5.67	0.039
263.6	-0.09937		-0.2895		+	-0.1306	6	-1482.63	2977.3	5.71	0.039

Table S5.3: Final nested AICc model selection for the GLM of avoidance behaviour across woodland habitats. Summary of results in Table 5.2.

Summary of variables in final selected models

Table S5.4

Parasite	Lag (month)	Parameter	Estimate	Standard Error	95% confidence intervals Lower	Upper
Directly transmitted						
Balantitidum coli	1	**Overlap (woodland)**	0.206	0.078	0.004	0.372
	1	NDVI	-0.268	0.112	-0.500	0.008
	1	Year	0.154	0.073	-0.083	0.110
	2	**Overlap (all habitats)**	-0.402	0.101	-0.601	-0.204
	2	NDVI	-0.219	0.118	-0.424	0.128
Medium amoeba	1	**Sex**	0.985	0.203	NA	NA
	1	**Year**	0.503	0.111	NA	NA
	1	**NDVI**	-0.915	0.149	NA	NA
	2	NDVI	-0.114	0.073	-0.183	0.097
	2	**Overlap (all habitats)**	-0.239	0.064	-0.365	-0.114
	2	**Year**	0.195	0.055	0.088	0.303
	2	Sex	0.184	0.119	-0.156	0.280
Small amoeba	1	**Age (poly 1)**	-2.035	2.765	NA	NA
	1	**Age (poly 2)**	8.121	2.720	NA	NA
	1	**Overlap (all habitats)**	-0.481	0.087	NA	NA
	1	**Overlap (woodland)**	0.532	0.096	NA	NA
	1	**Year**	0.905	0.092	NA	NA
	1	**NDVI**	-1.089	0.126	NA	NA
	2	Age (poly 1)	-3.971	3.251	-10.341	2.400
	2	**Age (poly 2)**	9.067	3.090	3.011	15.124
	2	**NDVI**	-1.401	0.235	-1.862	-0.940
	2	Overlap (woodland)	-0.206	0.142	-0.389	0.178
	2	Year	1.045	0.130	0.790	1.299
Indirectly transmitted						
Streptopharagus pigmentatus	1	Overlap (all habitats)	-0.133	0.084	-0.252	0.105
	1	Overlap (woodland)	0.196	0.101	-0.100	0.382
	1	Year	0.194	0.105	-0.112	0.378
	2	Overlap (all habitats)	-0.244	0.123	-0.474	0.127
	2	NDVI	-0.260	0.160	-0.500	0.196
Physaloptera caucasia	1	**Year**	0.292	0.095	NA	NA
	2	Sex	-0.467	0.289	-0.711	0.387
	2	Overlap (all habitats)	-0.212	0.144	-0.390	0.183
	2	Overlap (woodland)	0.256	0.152	-0.116	0.142
	2	Age (poly 1)	5.956	2.887	-4.372	9.066
	2	Age (poly 2)	0.610	2.514	-2.908	3.389
	2	Year	0.280	0.127	-0.070	0.540

Table S5.4: Final variable values for each binomial GLMM assessing the association between repeatedly visited habitats (all and woodland) with the presence or absence of directly and indirectly transmitted parasites. NA indicated that only one model was present in the final selected model. Variables in BOLD indicates conclusive associations, either through being present in a single final model or through the confidence intervals not crossing zero.

Table S5.5

Model	Variables	Estimate	Standard Error	95% confidence intervals	
				Lower	Upper
All habitats	**NDVI**	-0.049	0.008	NA	NA
	Small amoeba	-0.066	0.009	NA	NA
	Troop	0.071	0.017	NA	NA
	Year	-0.036	0.009	NA	NA
Woodland	**NDVI**	-2.775	0.033	-0.342	-0.213
	Troop	0.449	0.065	0.322	0.577
	Year	-0.139	0.010	-0.159	-0.119
	Small amoeba	0.089	0.036	-0.007	0.164
	B. coli	-0.100	0.036	-0.175	-0.017
	Medium amoeba	-0.074	0.035	-0.144	0.029

Table S5.5: Final variable values for two GLMs assessing the association between parasite presence with repeatedly visited habitats (all and woodland). NA indicated that only one model was present in the final selected model. Variables in BOLD indicates conclusive associations, either through being present in a single final model or through the confidence intervals not crossing zero.

APPENDIX THREE

SUPPLEMENTARY INFORMATION: CHAPTER SIX

Model selection for richness

Table S6.1.

Richness	Poisson	Proximity		Strength						
Intercept	NDVI 3 months	Proximity Strength		Age (poly 2)	Sex	df	logLik	AICc	delta	weight
1.075	0.03564	0.03032		+		6	-1759.24	3530.6	0	0.255
1.104	0.03204			+	+	6	-1759.36	3530.8	0.23	0.228
1.078	0.03479			+		5	-1760.51	3531.1	0.51	0.198
1.106				+	+	5	-1761.01	3532.1	1.5	0.12
1.076		0.02866		+		5	-1761.23	3532.5	1.94	0.097
1.079				+		4	-1762.4	3532.8	2.26	0.082
1.121	0.03367				+	4	-1763.85	3535.7	5.17	0.019

Table S6.1: Final model selection for parasite species richness and proximity strength.

Table S6.2

B. coli	Binomial	Grooming	Betweenness				
Intercept	NDVI 3 months	Sex	df	logLik	AICc	delta	weight
1.26	1.13	+	4	-570.929	1149.9	0	1

Table S6.2: Final model selection for presence / absence of *Balantidium coli* and grooming betweenness.

Table S6.3

Medium Amoeba	Binomial	Grooming	Betweenness						
Intercept	Dominance	Groom betweenness	NDVI 3 month	Age (poly 2)	Sex	df	logLik	AICc	delta	weight
3.679	-3.559	-0.3272	1.136	+	+	8	-430.558	877.3	0	0.879
3.406	-3.385		1.123	+	+	7	-433.555	881.2	3.96	0.121

Table S6.3: Final model selection for presence / absence of medium amoeba and grooming betweenness.

Table S6.4

Small Amoeba	Binomial	Grooming	Betweenness						
Intercept	Dominance	NDVI 3 months	Age (poly 2)	Sex	df	logLik	AICc	delta	weight
-0.6301	1.243	2.313	+	+	7	-524.443	1063	0	0.399
0.0436	1.495	2.302	+		6	-525.804	1063.7	0.7	0.282
0.00508		2.196	+	+	6	-526.021	1064.1	1.13	0.227
0.8127		2.202	+		5	-527.926	1065.9	2.92	0.093

Table S6.4: Final model selection for presence / absence of small amoeba and grooming betweenness.

Table S6.5

S. pigmentatus	Binomial	Proximity	Betweenness				
Intercept	Dominance	Sex	df	logLik	AICc	delta	weight
2.444	-1.144		3	-448.838	903.7	0	0.763
2.086		+	3	-450.561	907.1	3.45	0.136
1.85			2	-451.873	907.8	4.06	0.1

Table S6.5: Final model selection for presence / absence of *Streptopharagus pigmentatus* and proximity betweenness.

Table S6.6

P. caucasia	Binomial	Grooming	Strength						
Intercept	Groom Strength	NDVI 3 months	Age (poly 2)	Sex	Troop	df	logLik	AICc	delta	weight
-1.931	0.1699	-0.143	+			6	-436.758	885.6	0	0.215
-1.931	0.1786		+			5	-437.785	885.6	0.03	0.212
-1.941		-0.1523	+			5	-438.043	886.1	0.55	0.164
-1.94			+			4	-439.215	886.5	0.87	0.139
-2.09	0.2316	-0.1682			+	5	-438.898	887.9	2.26	0.07
-2.086	0.2413				+	4	-440.372	888.8	3.19	0.044
-1.72	0.2031	-0.1775		+		5	-439.407	888.9	3.27	0.042
-1.896	0.2283	-0.1676				4	-440.427	888.9	3.29	0.041
-1.89	0.2383					3	-441.865	889.8	4.16	0.027
-1.872		-0.1904		+	+	5	-440.3	890.7	5.06	0.017
-1.679		-0.1914		+		4	-441.395	890.8	5.23	0.016
-2.092		-0.181			+	4	-441.58	891.2	5.6	0.013

Table S6.6: Final model selection for presence / absence of *Physaloptera caucasia* and grooming strength

Table S6.7

B. coli	Poisson	Proximity	Betweenness			
Intercept	NDVI 3 months	df	logLik	AICc	delta	weight
0.1688	0.2382	3	-204.56	415.3	0	1

Table S6.7: Final model selection for abundance of *Balantidium coli* and proximity betweenness.

Table S6.8

Medium Amoeba	Poisson	Proximity	Betweenness						
Intercept	Dominance	NDVI 3 months	Age (poly 2)	Sex	df	logLik	AICc	delta	weight
0.9333	-0.7584	0.1238	+	+	7	-240.1	495	0	0.837
0.9109	-0.6863		+	+	6	-243.2	498.9	3.89	0.12
0.953	-0.4997	0.09948	+		6	-244.2	500.9	5.89	0.044

Table S6.8: Final model selection for abundance of medium amoeba and proximity betweenness.

Table S6.8

Small Amoeba	Poisson	Proximity	Betweenness				
Intercept	NDVI 3 months	Age (poly 2)	df	logLik	AICc	delta	weight
0.07943	0.331	+	5	-216.19	442.8	0	1

Table S6.8: Final model selection for abundance of medium amoeba and proximity betweenness.

Table S6.9

S. pigmentatus	Gaussian	Proximity	Betweenness								
Intercept	Dominance	NDVI 3 months	Proximity	Age (poly 2)	Sex	Troop	NDVI:Proximity	df	logLik	AICc	delta	weight
79.98	-56.06	-5.946	12.65	+	+	+	8.547	11	-908.373	1840.6	0	0.933
77.39	-53.09	-7.597	9.233	+	+	+		10	-912.161	1845.9	5.25	0.067

Table S6.9: Final model selection for intensity of *Streptopharagus pigmentatus* and proximity betweenness.

Table S6.10

P. caucasia	Gaussian	Proximity	Strength								
Intercept	Dominance	NDVI 3 months	Proximity	Age (poly 2)	Sex	Troop	df	logLik	AICc	delta	weight
4.343	-2.445		1.451	+	+	+	9	-470.112	959.5	0	0.253
4.327	-2.601		1.487	+		+	8	-471.379	959.8	0.28	0.22
5.231	-2.293		1.428	+	+		8	-472.387	961.8	2.29	0.08
3.539		-0.6678	1.191	+	+	+	9	-471.283	961.8	2.34	0.078
3.446			1.241	+	+	+	8	-472.449	961.9	2.42	0.076
5.216	-2.62		1.499	+			7	-473.702	962.2	2.69	0.066
3.059			1.337	+		+	7	-473.884	962.5	3.06	0.055
3.981	-0.4267	-0.7053		+	+	+	9	-472.246	963.8	4.27	0.03
4.437		-0.6737	1.175	+	+		8	-473.459	963.9	4.44	0.028
4.057	-0.862			+	+	+	8	-473.502	964	4.52	0.026
4.357			1.231	+	+		7	-474.642	964.1	4.57	0.026
3.828		-0.7252		+	+	+	8	-473.891	964.8	5.3	0.018
3.938			1.346	+			6	-476.213	965	5.52	0.016
3.884	-1.642			+		+	7	-475.215	965.2	5.72	0.014
3.736				+	+	+	7	-475.229	965.2	5.75	0.014

Table S6.10: Final model selection for intensity of *Physaloptera caucasia* and proximity strength.

APPENDIX FOUR

SUPPLEMENTARY INFORMATION: CHAPTER SEVEN

Table S7.1

Intercept	MHC richness	MHC v NDVI	df	logLik	AICc	delta	weight
1.375	-0.0009066	-0.01608	6	-404.822	821.7	0	1

Table S7.1. Final model selection for richness and genetic diversity

Table S7.2

Intercept	MHC richness	MHC v NDVI	df	logLik	AICc	delta	weight
1.741	0.003404	-0.05024	5	-695	1400.6	0	0.588
1.694			3	-698	1401.3	0.71	0.41

Table S7.2. (A) Final model selection for *Streptopharagus* binomial

Intercept	df	logLik	AICc	delta	weight
4.074	4	-892.049	1792	0	1

Table S7.2 (B) Final model selection for *Streptopharagus* intensity

Table S7.3

Intercept	Troop	df	logLik	AICc	delta	weight
-2.069	+	4	-558.8	1126	0	0.838
-1.877		3	-561.5	1129	3.28	0.162

Table S7.3 (A) Final model selection for *Physaloptera* binomial

Intercept	Inbreeding	Troop	df	logLik	AICc	delta	weight
1.051	0.1788	+	6	-437	886	0	0.916
1.079		+	5	-440	890.8	4.78	0.084

Table S7.3 (B) Final model selection for *Physaloptera* intensity

Table S7.4

Intercept	Inbreeding	df	logLik	AICc	delta	weight
1.961	-0.1055	4	-712.422	1433	0	0.553
1.976		3	-713.641	1433	0.43	0.447

Table S7.4 (A) Final model selection for *Balantidium* binomial

Intercept	df	logLik	AICc	delta	weight
1.851	4	-1130.059	2268.2	0	1

Table S7.4 (B) Final model selection for *Balantidium* intensity

Table S7.5

Intercept	ply(Age,2)	Sex	df	logLik	AICc	delta	weight
1.053	+	+	6	-408.819	829.7	0	0.644
1.002		+	4	-411.429	830.9	1.19	0.356

Table S7.5 (A) Final model selection for medium amoeba binomial

Intercept	MHC richness	Troop	MHC v NDVI	df	logLik	AICc	delta	weight
1.206	0.01243	+	0.01284	7	-2464	4941.8	0	0.471
1.24	0.01169		0.01407	6	-2465	4942.9	1.15	0.265
1.272		+		5	-2467	4943.6	1.81	0.191
1.306				4	-2469	4945.5	3.75	0.072

Table S7.5 (B) Final model selection for medium amoeba intensity

Table S7.6

Intercept	MHC richness	MHC v NDVI	df	logLik	AICc	delta	weight
0.0461	-0.1088	-0.2431	5	-364.979	740	0	1

Table S7.6 (A) Final model selection for small amoeba binomial

Intercept	df	logLik	AICc	delta	weight
1.291	4	-43.928	95.9	0	1

Table S7.6 (B) Final model selection for small amoeba intensity

APPENDIX FIVE

Supporting information for the potential environmental transmission of gastrointestinal parasite protists, and the analysis of Tsaobis soil and water samples for their cysts

BACKGROUND

The gastrointestinal protozoa that infect the Tsaobis baboon population include *Balantidium coli*, various *Entamoeba* species, *Chilomastix mesnili*, and *Iodamoeba bütschlii*. All these species are reported to be directly transmitted (i.e. without an intermediate host or vector) (Chapter 2, Table 2.1). Specifically, their transmission is thought to be through the faecal-oral route, at least in humans, (Bogitsh, 2018; Martinez-Palomo, 1993; Zaman, 1993) although this mode of transmission has also been indicated in baboons (Appleton & Brain 1995), including with a potential build-up of faecal matter in the environment (Hausfater & Meade, 1982), and either remaining in the soil or leaking into water sources. Host-to-host contact transmission is also possible, since the social network positions of baboons have been correlated with microbiome diversity (Tung, 2015) and the infectious stages of these gastrointestinal parasites may be transmitted in the same way, but the findings of this thesis are not consistent with such a transmission route (see Chapter six). Finally, mechanical vectors might also facilitate parasite transmission. These gastrointestinal protozoa can survive in the digestive tracks of flies and cockroaches for long periods (Bogitsh, 2018). However, there are no data available to assess this possibility one way or the other.

In other locations, *Balantidium coli* and *Entamoeba* spp. have been observed in water sources (Ajeagah, 2013; Alexander et al., 2013) *Entamoeba histolytica* is known to survive in water for one month, and in faeces for around 12 days, with thermal death occurring at around 50^{oC} (Bogitsh, 2018). If the parasite cysts are entering the water sources at our study site, then potentially the cysts will persist for longer in the environment. The movement of these cysts from faeces may depend primarily on rainfall to wash the eggs away (Freeland, 1980); or from the breakdown of the faecal matter. The breakdown of faecal matter will also inhibit the ability of a baboon to avoid the cysts.

This is also of potential interest in the transmission of the eggs of the two common helminth parasites in the Tsaobis baboon population: *Streptopharagus pigmentatus* and *Physaloptera*

caucasia. However, both of these parasites are believed to be transmitted through insect vectors (see Chapter 2), most likely Orthopteran insects on which the baboons forage. How the orthopterans come to consume the eggs expelled from the baboons is unknown, but it is possible they feed on the baboons' dried faeces if it also contains the remains of preferred plant foods.

METHODS

Soil and water samples were collected during October 2014. A total of 18 water and soil locations were each sampled three times. This resulted in the collection of 24 water samples and 30 soil samples. These samples were collected from three types of sites: waterholes; soil from sleeping sites; and soil from grooming/resting sites (Fig. A1.1). The location of each sampling site was recorded using a handheld GPS (global positioning system), and these are plotted on Fig. A1.2.

Fig. S5.1. Photos of four of the water and soil sampling locations in October 2014. Top left: sleeping cliff, top right: shady grooming/resting site (under tree), bottom left: artificial waterhole, bottom right: natural waterhole. Photo credit: Alex Lee.

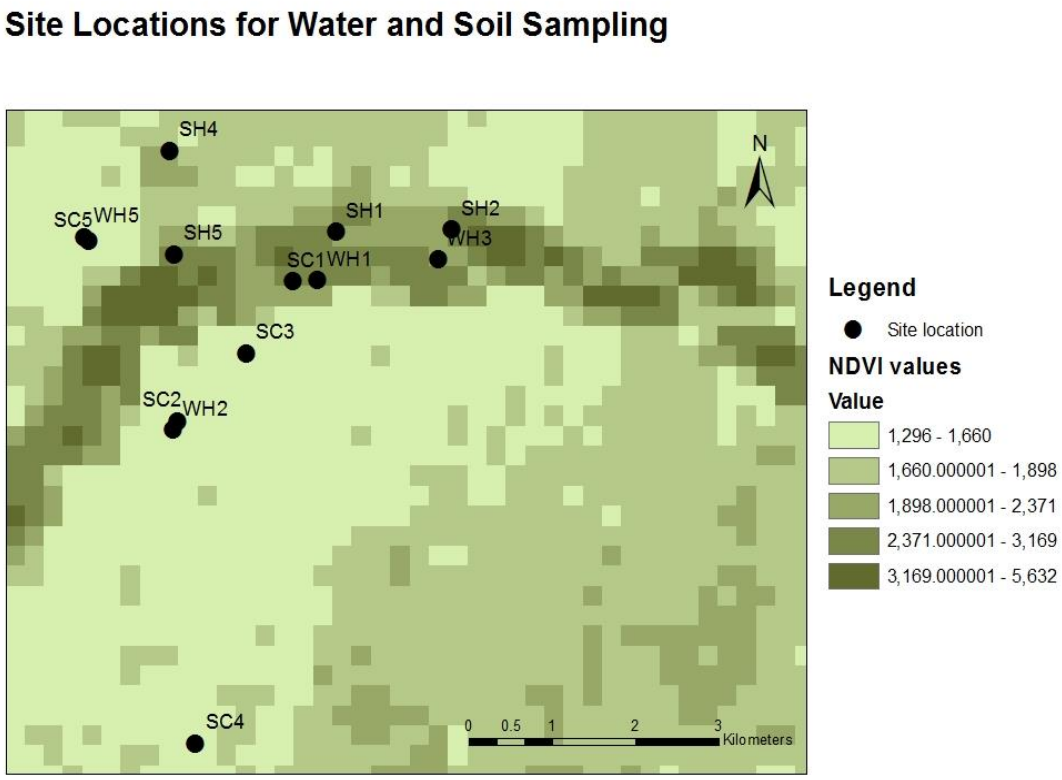

Fig. S5.2. GPS points of the sites of water and soil sampling for October 2014. Points are plotted against NDVI values to show the range of environments sampled: the desert hills and plains = light green, the woodlands of the ephemeral Swakop riverbed = dark green.

The locations of these sites were based on the activities of the baboon troops. Daily observations of the troops had been occurring prior to the environmental sampling, and those areas that had been frequently used in recent weeks were sampled. Based Hausfater & Meade's (1982) hypothesis that parasites accumulate under sleeping locations, we sampled below and on sleeping cliffs. Water is a restricted resource at this study site and the few waterholes that are available are frequently revisited. Water is also known to be a prominent source of enteropathogenic protozoa transmission (Ajeagah, 2013; Kaur & Singh, 2009) and for this reason we sampled the water that the baboon troops drink. Finally, the baboons also spend a lot of time in shady areas where they rest and groom during the day, and given the possibility of faecal and parasite accumulation in these locations, these areas were also sampled. Such shaded areas may also protect the cysts from desiccation, as the shade provides a much more steady temperature range in semi-arid areas of Namibia,

providing a buffer from the extreme temperatures which is likely to increase the cysts' survival rate (Appleton, 1995).

Sample collection: water

Water from four different locations where the baboons were known to drink were sampled for cysts. The samples were collected from both the body of the water and the sediment at the bottom. Each of these types of sample was repeated three times, resulting in 24 samples. At each site, 3ml of water was pipetted into a centrifuge tube that contained 2ml 10% formalin to preserve any cysts present. On returning to camp, Sheather's sugar solution was added to the tubes until a meniscus of the liquid appeared at the rim of the tube. A coverslip was then rested on the top of the tube and the contents allowed to settle and rise onto the coverslip. The coverslip was then placed onto a microscope slide for observation under phase contrast, then scanned systematically until all the slide had been assessed.

Sample collection: soil

Soil from five sleeping cliffs and five grooming/resting sites were collected, and at each site three replicate samples were taken, producing 30 samples. Roughly $2cm^2$ of soil were added into centrifuge tubes that contained 2ml 10% formalin and shaken to separate any clumps of soil. Using flotation on sandy soil samples is also an effective way to extract *Toxocara* eggs from the environment (Nunes et al., 1994), and due to the sandy consistency of the soil present at Tsaobis (Cowlishaw, 1997) it is likely that this technique should be effective in this study location. Once the samples were back at camp, Sheather's sugar solution was added to the tubes until a meniscus of the liquid appeared at the rim of the tube. A coverslip was then rested on the top of the tube and the contents allowed to settle and rise onto the coverslip. The coverslip was then placed onto a microscope slide for observation under phase contrast, then scanned systematically until all the slide had been assessed.

RESULTS

A total of four *Entamoeba* cysts were found using this method (see Fig. A1.3). Due to their small size, I identified them as *Entamoeba hartmanni.* These were found in one soil sample, in a grooming/resting location, and in two water samples (Table A1.1). In addition I recorded

other microorganisms and plant material, such as pollen (Fig. A1.3). Some of the material in the sample resembled eggs or cysts, but I was unable to come to a conclusive identification in all cases.

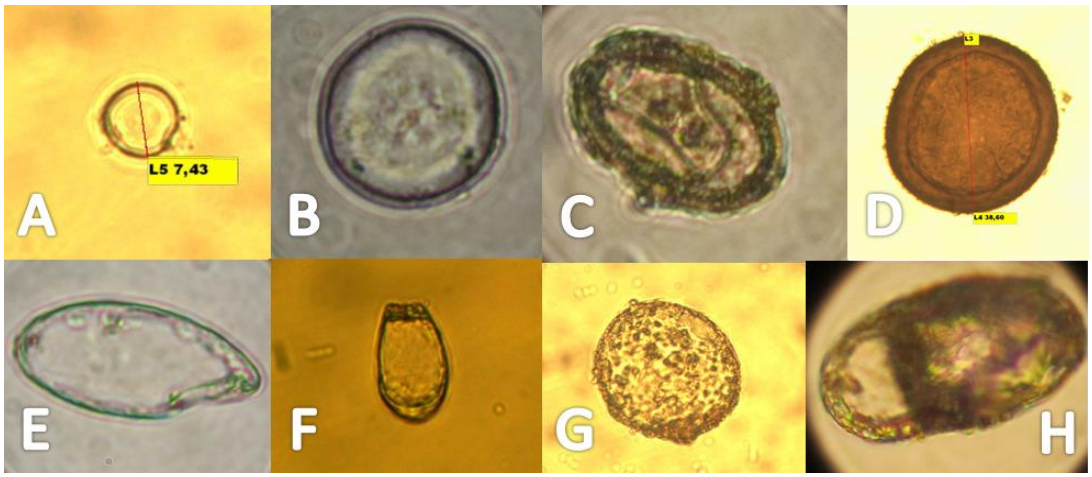

Figure. S5.3. Images from soil and water samples. A – From sample WH5Bb, a possible cyst from an *Entamoeba* species, most likely *Entamoeba hartmanni*. B – From sample SC3a, a possible cyst from an *Entamoeba* species. C-D – Pollen. E – Testate amoeba *Trinema lineare*. F – Testate amoeba *Euglypha rotunda*. G – Testate amoeba *Cyclopyxis* sp. H – Testate amoeba (*Centropyxis aerophile*).

Sample Code	Site	Site type	Sample Repeat	Sample weight (g)	Pathogens presence/ absence	Pathogens
SC1	Baboon Hill	Sleeping cliff	1	3.90	absent	
SC1	Baboon Hill	Sleeping cliff	2	3.51	absent	
SC1	Baboon Hill	Sleeping cliff	3	4.56	**present**	Unidentified Amoeba
SC2	Leopardquelle	Sleeping cliff	1	1.62	absent	
SC2	Leopardquelle	Sleeping cliff	2	1.57	absent	Egg, maybe Toxocara
SC2	Leopardquelle	Sleeping cliff	3	1.7	absent	
SC3	Leopardberg	Sleeping cliff	1	2.67	absent	

SC3	Leopardberg	Sleeping cliff	2	2.32	absent	
SC3	Leopardberg	Sleeping cliff	3	2.51	absent	
SC4	The Bowl	Sleeping cliff	1	3.03	absent	
SC4	The Bowl	Sleeping cliff	2	2.53	absent	
SC4	The Bowl	Sleeping cliff	3	2.62	absent	
SC5	The Dog Bowl	Sleeping cliff	1	2.13	absent	
SC5	The Dog Bowl	Sleeping cliff	2	1.52	absent	
SC5	The Dog Bowl	Sleeping cliff	3	2.29	absent	
SH1	*Faidherbia* (near camp)	Under tree	1	2.27	**present**	Unidentified egg
SH1	*Faidherbia* (near camp)	Under tree	2	2.27	absent	
SH1	*Faidherbia* (near camp)	Under tree	3	2.25	absent	
SH2	*Faidherbia* (Fritz Stark)	Under tree	1	2.93	absent	
SH2	*Faidherbia* (Fritz Stark)	Under tree	2	3.52	absent	
SH2	*Faidherbia* (Fritz Stark)	Under tree	3	3.33	**present**	1 x *Entamoeba* spp
SH3	*Faidherbia* (UNK003)	Under tree	1	2.39	absent	
SH3	*Faidherbia* (UNK003)	Under tree	2	2.74	absent	

SH3	*Faidherbia* (UNK003)	Under tree	3	2.26	absent	
SH4	*Faidherbia* (Gaumikaub bend)	Under tree	1	3.03	absent	
SH4	*Faidherbia* (Gaumikaub bend)	Under tree	2	2.12	absent	
SH4	*Faidherbia* (Gaumikaub bend)	Under tree	3	2.40	absent	
SH5	*Faidherbia* (Gaumikaub mouth)	Under tree	1	3.28	absent	
SH5	*Faidherbia* (Gaumikaub mouth)	Under tree	2	3.11	absent	
SH5	*Faidherbia* (Gaumikaub mouth)	Under tree	3	2.83	absent	
WH1B	Baboon Hill	Waterhole (water)	1	3.23	absent	
WH1B	Baboon Hill	Waterhole (water)	2	3.19	absent	
WH1B	Baboon Hill	Waterhole (water)	3	3.24	absent	
WH1S	Baboon Hill	Waterhole (sediment)	1	3.02	absent	
WH1S	Baboon Hill	Waterhole (sediment)	2	3.16	**present**	1 x *Entamoeba* spp
WH1S	Baboon Hill	Waterhole (sediment)	3	3.28	absent	
WH2B	Leopardquelle	Waterhole (water)	1	3.28	absent	
WH2B	Leopardquelle	Waterhole (water)	2	3.51	absent	
WH2B	Leopardquelle	Waterhole (water)	3	3.15	absent	
WH2S	Leopardquelle	Waterhole (sediment)	1	3.22	**present**	2 x *Entamoeba* spp
WH2S	Leopardquelle	Waterhole (sediment)	2	3.04	absent	

WH2S	Leopardquelle	Waterhole (sediment)	3	3.19	absent	
WH3B	Fritz Stark trough	Waterhole (water)	1	2.89	absent	
WH3B	Fritz Stark trough	Waterhole (water)	2	2.95	absent	
WH3B	Fritz Stark trough	Waterhole (water)	3	3.16	absent	
WH3S	Fritz Stark trough	Waterhole (sediment)	1	3.12	absent	
WH3S	Fritz Stark trough	Waterhole (sediment)	2	3.09	absent	
WH3S	Fritz Stark trough	Waterhole (sediment)	3	2.82	absent	
WH5B	The Dog Bowl	Waterhole (water)	1	3.01	absent	
WH5B	The Dog Bowl	Waterhole (water)	2	2.94	**present**	Unidentified amoeba
WH5B	The Dog Bowl	Waterhole (water)	3	3.07	absent	
WH5S	The Dog Bowl	Waterhole (sediment)	1	3.05	**present**	Unidentified amoeba
WH5S	The Dog Bowl	Waterhole (sediment)	2	3.09	**present**	Egg, maybe Toxocara
WH5S	The Dog Bowl	Waterhole (sediment)	3	3.26	absent	

Table S5.1. List of the samples collected, repeated in batches of three for each location. Sample types fall into the categories of: Sleeping cliff (gravel below or around sleeping locations); Under tree (known grooming/resting locations in the shade); Waterhole water (sample of water taken from known drinking location) and Waterhole sediment (sample of soil taken from around the waterhole).

DISCUSSION

This method was capable of extracting microorganisms from the environment: the presence of numerous testate amoeba and pollen demonstrated the potential for this technique to detect parasitic eggs or cysts from such samples where present. There were a few small amoeba (*Entamoeba hartmanni*), which suggests that protist cysts do persist within the environment. Not only were they present in the water samples (three of the four cysts), but

there was also evidence that they persisted in the soil. Interestingly, there were no cysts found in any of the sleeping cliff samples.

My ability to detect parasites in the environment may have been restricted by the methodology used. Firstly, only low numbers of cysts were extracted due to the small amounts of soil and water collected. In other studies, the density of protists in the environment was also generally fairly low. For example, (Ajeagah, 2013) found *Entamoeba* spp. at a density of 1-25 cysts per litre when present, and *Balantidium coli* at 2-13 cysts per litre. However, as illustrated in Fig. A1, the amount of water present in the environment was too low to sample at high volumes. The technique used by Ajeagah (2013) required a litre of water, but at Tsaobis this was not feasible. Likewise, for the soil collection using flotation, Nunes et al. (1994) used 50 grams of soil, but restrictions imposed by my equipment meant that this amount of soil was also unfeasible for this project. Finally, further equipment restrictions prevented me from following alternative parasite extraction protocols. For instance, other studies have suggested that centrifugation is necessary for the effective flotation of eggs from the sediment (Zenner et al., 2002).

Despite these constraints, I was able to extract cysts from the environmental samples, suggesting that they do persist in the landscape. Whether this is true for are any other species apart from *E. hartmanni* is yet to be seen. There was no evidence of any of the larger protist species, despite the fact that *Balantidium coli* and *Entamoeba histolytica*/*dispar* are much more common in the Tsaobis baboon population (Benavides et al., 2012). It is possible that the cysts of these species may have been detected with further sampling, especially at other times of the year if these particular parasites require cooler or wetter environmental conditions to survive. It also remains possible that these protists are transmitted more directly through contact (but see Chapter 6) or through indirect transmission. In the latter case, Tatfeng et al. (2005) have reported that cockroaches (*Diploptera punctate*) are able to be infected with *Entamoeba histolytica* and *Balantidium coli*. Indirectly transmitted parasites can be sheltered from extreme environmental conditions, and might help to explain the ability of these pathogens to persist in these semi-arid conditions. Nevertheless, further research is required to obtain a more complete picture of the spatial and temporal distribution of parasite infectious stages in the environment at Tsaobis.

APPENDIX SIX

What happens after defecation? Faecal degradation rate and invertebrate communities

INTRODUCTION

The defecation of faeces is a primary method for the deposition of parasite eggs and cysts into the environment. Where previous studies have monitored the dispersion of these infectious stages after defecation, it was noted that generally the eggs and cysts remain localised to the faeces (Ezenwa, 2004b). Therefore the location of the faeces, and the interactions of species with the faeces, are important for considering the dispersion of parasites and has implications for the spatial transmission of parasites. For example, the transmission of trematodes from wading birds to mangrove snails (*Cerithidea scalariformis*) is greatly dictated by the defecation location of the birds. The snails that were experimentally placed in closer proximity to the faeces were exposed to the more infectious stages of trematodes (Smith, 2001). If, however, the faecal matter can be dispersed, then the spread of parasite eggs/cysts can be proliferated across the environment. Faeces can be dispersed through contact with animals, or through the microhabitat: heavy rainfall may wash away faecal matter (Stromberg, 1997). Additionally, any invertebrate species feeding on faeces will displace faecal matter and may ultimately act as intermediate hosts or mechanical vectors for any parasite infectious agents present in the faeces (Boze et al., 2012). Since infectious eggs/cysts are transferred to a new host either through the faecal-oral route, through their distribution into the environment, or through intermediate hosts or vectors contacting the faeces, understanding the distribution of faecal contamination is important if we are to understand parasite transmission.

Here I conducted a preliminary study into the decay and dispersal of faeces from baboons in a semi-arid environment. There are three aims of this study: (1) monitoring the persistence of faeces in the environment; (2) identifying invertebrates that contact the faeces; (3) explore which factors influence the presence of invertebrates.

METHODS

Data collection occurred from October 2014 through to January 2015. Faeces were collected in their entirety and were transported immediately from the site of defecation to an experimental site for monitoring. Information about which individual baboon defecated, along with the date and time of collection, and the size, colour, and consistency of the faeces, was recorded. For details of the study location and species, see Chapter Four.

Faecal degradation monitoring

The faeces were placed in four different environmental conditions: on either sand or gravel substrate, and each of these were either exposed to sunlight or under dappled shade conditions. To monitor the faecal samples, they were surrounded by a metal mesh, with the gaps between the wiring significantly larger than the invertebrates or small mammals that may feed on the sample. At regular intervals, starting at hourly, and reducing to weekly (specific schedule shown in Table S6.1), I recorded the size, colour, and consistency of the faeces. Volume was calculated from the multiplication of the length, width, and height of the faeces and is therefore an estimation of the actual volume. During the next field season, in May 2015, faecal samples were observed again to see if they were still present after the rainy season.

Event	Date	Time of observation(s)
October collection (1)	15/10/2014	09:00; 15:00
October collection (2)	16/10/2014	09:00; 15:00
Observation	18/10/2014	19:00
Observation	23/10/2014	18:00
November collection (1)	14/11/2014	06:00; 15:00
November collection (2)	15/11/2014	06:00; 15:00
Observation	17/11/2014	15:00
Observation	20/11/2014	08:00
Observation	29/11/2014	15:00
December collection (1)	14/12/2014	05:30; 09:00; 15:00
December collection (2)	15/12/2014	05:30; 09:00; 15:00
Observation	30/12/2014	12:00
Observation	03/01/2015	10:40
Observation	07/01/2015	16:00
January collection (all)	14/01/2015	05:00; 13:00; 17:00

Table S6.1. Dates and times of when faecal samples were collected and monitored.

Invertebrate monitoring

The invertebrates feeding on the faeces were recorded on all months that faecal samples were collected. Where possible invertebrates were identified to species level based on morphology, with identification of insects guided by Picker (2012).

RESULTS

In total 32 faeces were collected and placed into one of four habitat types: gravel, shaded or unshaded, and sandy, shaded or unshaded. These four different habitat types exposed the faeces to different microhabitat conditions, so that the rate of degradation and the number of invertebrates present could be monitored in different environments. The specific details of the temperature differences across microhabitats are described in Chapter Five. Faeces were then monitored for changes in size and invertebrates present.

Degradation of faeces

All faeces remained in the experimental locations during the observation period (maximum time of monitoring: 1469 hours / 61 days), and many of the faeces showed no change in size (n=8). The greatest change in size being a faeces where only 12% of the original volume remained (from 90cm^2 to 10.5cm^2). On average, almost half (47%) of the faeces remained after monitoring with no apparent differences between locations (gravel, no shade = 52%; gravel, shady = 41%; sand, no shade = 45%; sand, shady = 50%). Changes in the volume of the faeces across time are illustrated in Figure S6.1. Additionally, the faeces were still present during the following field season in May 2015, despite the rainy season occurring between these two periods. All faeces appeared to desiccate, changing colour from green or light brown to dark brown, between the first and second observation. Therefore, somewhere in the first few hours the faeces began to lose moisture.

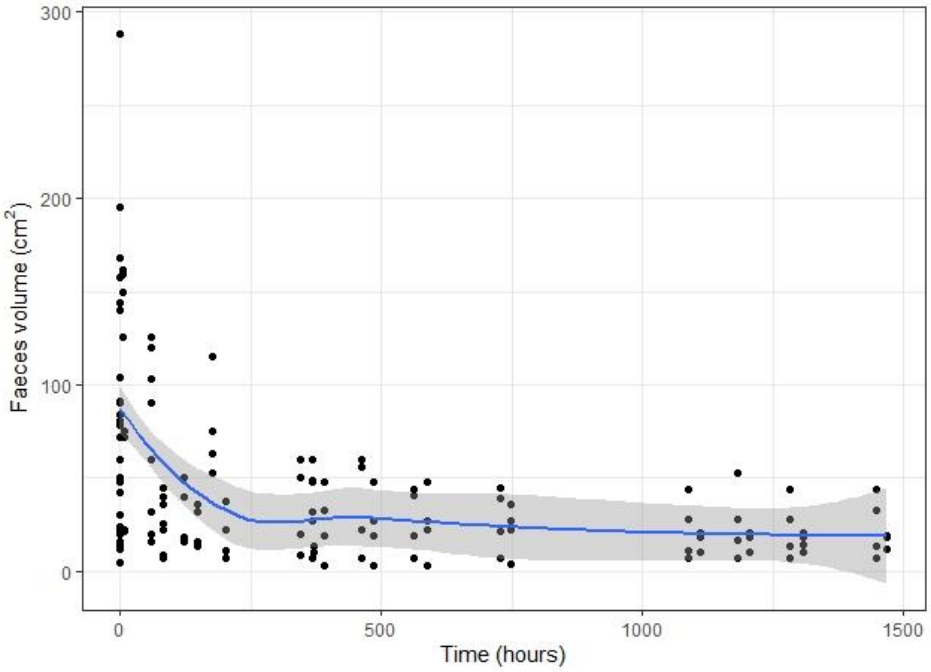

Figure. S6.1 Faeces volume (cm^2) measured at different times post sample collection, with the moving regression illustrating the general trend over time.

Invertebrate monitoring

The most common invertebrate to visit the faeces were flies, which includes the following species: *Musca domestica*, *Chrysomya chloropyga*, *Lucilia* spp., *Sarcophaga pachtyli*, along with an unknown fly species. There is evidence of beetles consuming the faeces, with two darkling beetles *Stenocara gracilipes* and *Stenocara dentate* recorded visiting the faeces. In addition, there are a few species of ants that are present around the faeces, most unidentified but includes *Camponotus fulvopilosus*. Invertebrates respond quickly to defecation events and the number of individuals reacting to the faeces declined within hours (see Fig. S6.2A). Invertebrates appeared to be more present in sandy habitats that were not shaded, and the fewest invertebrates present in either of the shaded locations (i.e. gravel dappled shade and sand dappled shade), see Fig. S6.2B. Another observation was the preference that invertebrates showed to some faeces over others, despite being collected at the same time. Figure S6.3 provides an example of these differences. At the first observation, which occurred as soon as the faeces in placed in the experimental habitat, 66% of faeces were visited by invertebrates in the first 5 minutes. Of these 32 samples, 11 (34%) had no invertebrates visiting immediately, and those that did have invertebrates present were visited by a maximum of 100 individuals, and a minimum of 1 individual (mean across all samples = 9). All species present in the immediate observation were flies (order Diptera),

with other species such as ants (order Hymenoptera) and beetles (order Coleoptera) visiting a few hours after the faeces was deposited.

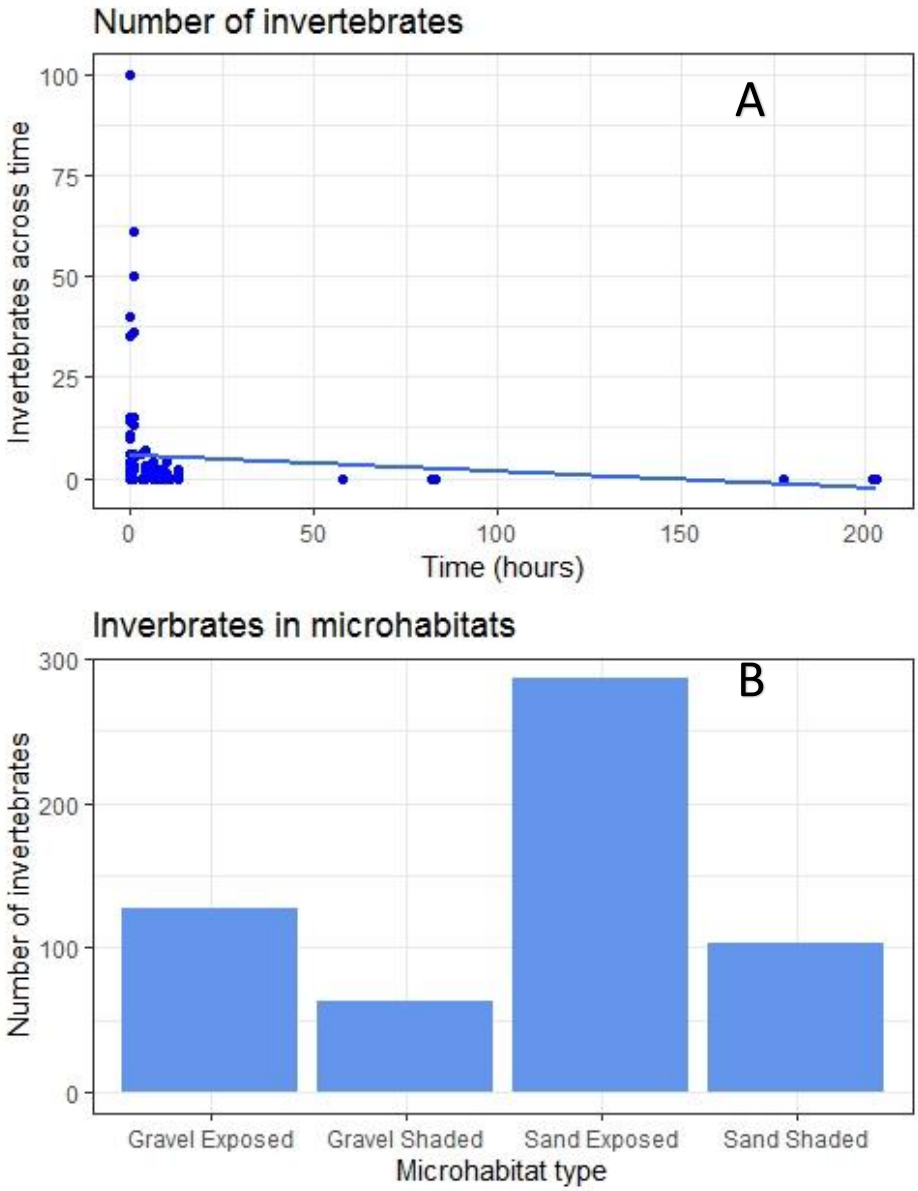

Figure S6.2: Plots of the number of invertebrates contacting the faecal samples with (A) showing the changes in invertebrates across time; and (B) showing the distribution of invertebrates across different habitat types.

Figure S6.3: Photograph of two faecal samples placed in the unshaded sandy location. This is illustrative of the preferences of invertebrates (here blowflies: *Chrysomya chloropyga*) in contacting different faeces.

DISCUSSION

In this preliminary study I documented the rate at which baboon faeces decay in a semi-arid environment. From the collection of 32 faecal samples, I was able to monitor the change in size and the invertebrates present on the faeces. Two sets of faeces were placed into four different habitat types in order to control for the influence of exposure to microhabitat conditions on faeces degradation and invertebrate communities present.

Faecal degradation monitoring

Of the 32 faecal samples collected between October 2014 to January 2015, all were still present at the end of the monitoring period. Additionally, faeces were all still present following the rainy season when observed in May 2015. This is inconsistent with other studies, which have assumed that faeces decay at an exponential rate, or in an 'instantaneous mortality rate' (Barnes & Barnes, 1992). At other study sites, the persistence of baboon faeces under sleeping trees greatly varied depending on the weather conditions (Hausfater, 1982), which suggests that the decay rate is influenced by the environment. This was evident for other primate systems that rainfall was a key factor in removing faeces, either noted through direct observation (Andresen, 1999), or assumed from changes to their movement behaviour: mandrills (*Mandrillus sphinx*) were more likely to return to a location after rainfall (Poirotte, 2017a); and mangabeys (*Cercocebus albigena*) repeatedly used areas of their home

range after rainfall (Freeland, 1980). However, the theories that rain downpours are important for dispersing parasites, via faeces, into the environment do not seem to be important for this study site. Therefore, the spatial clustering of host movement is likely to play a key role in parasite transmission, as illustrated in Chapter five.

Invertebrate monitoring

Faeces were frequently visited by invertebrates, with fly (Diptera) species present within the first five minutes, and flies, ants (Hymenoptera), and beetles (Coleoptera) present a few hours later. Generally, few invertebrates were present on the faeces in the following days. At other study sites, changes in faeces volume was influenced by diurnally-active dung beetles (Hausfater, 1982), and likewise it appears that beetles were responsible for consuming at least some of the faeces (Figure S6.4).

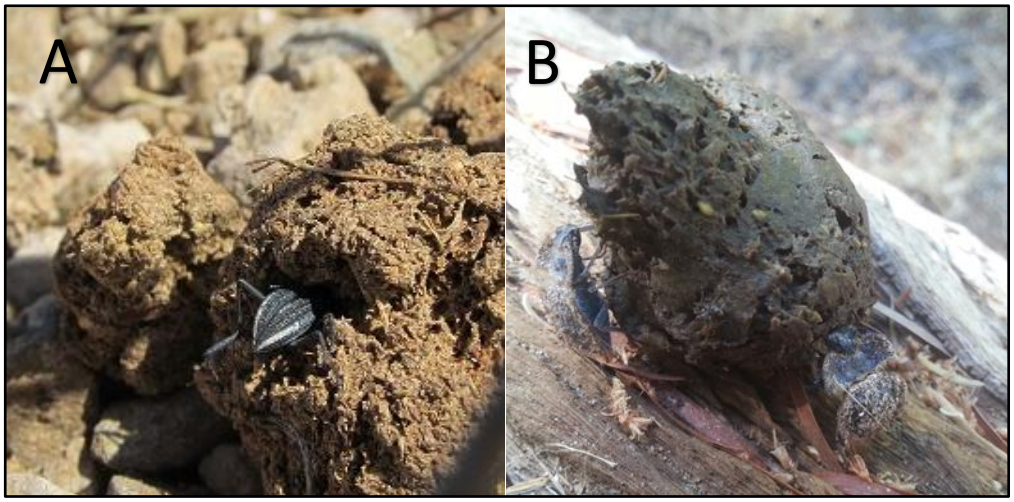

Figure S6.4. Examples of beetles (Coleoptera) consuming and contacting baboon faeces: (A) photograph of a *Stenocara gracilipes* entering a desiccated baboon faeces from the unshaded gravel microhabitat; (B) photograph of two unidentified dung beetles (*Scarabaeus (Pachysoma)* sp.) contacting and manipulating a fresh baboon faeces.

Implications for parasite transmission

In the Tsaobis Baboon Project study site, faeces are exposed to harsh conditions. Rainfall is minimal and highly seasonal (see Chapter three) and so for the most part the faeces are not washed away and rely on decaying in the sun or the removal through invertebrates or larger

species. The continuous presence of faeces in the habitat may have implications for parasite transmission. If the parasite infectious stages are able to remain viable despite the desiccation of the faeces, then the possibility of infection from areas frequently visited by the host remain high risk for parasite transmission regardless of the season. However, if invertebrates play a role in the transmission of these infectious stages, then the risk of transmission is not spatially limited, and instead the invertebrates can disperse these infectious stages across the host's range. From these observations it became apparent that multiple invertebrate species contact the faeces. Many of these species are not consumed by the baboons (*personal observation*), and therefore may not act as intermediate hosts, but instead the faeces are contacted by species that are likely to act as mechanical vectors for parasite transmission (e.g. Oyerinde, 1976; Zohdy & Schwartz, 2019).

Overall, persistence of the faeces and the distribution of faeces in the Tsaobis study site is higher than other study sites. This has implications for avoidance behaviours: if baboons are able to see the location of the faeces, with them persisting for weeks at a time, then avoiding these parasite transmission hotspots might prove easier than at other study sites (e.g. Andresen, 1999; Freeland, 1980a; Hausfater & Meade, 1982; Poirotte, Benhamou, et al., 2017). In cases where faeces have decayed or been washed away, the infectious stages of parasites may still persist in the soil (Sloss et al., 1994) and the host may be unable to avoid the hotspots of transmission through environmental cues. Whether this translates to differences in parasite survival and parasite dispersion is unknown, and further research is needed to explore this relationship. However, from other studies (Hausfater, 1982) we might expect that the parasite eggs and cysts remain viable even after the faeces has desiccated. Undoubtedly, further research is needed in order to understand the consequences of faeces persistence and the invertebrate communities on parasite survival and dispersion in the environment.

Attributions

Details of the contributions from others in order to complete this thesis.

Thesis

This thesis is a product of the long-term dataset collected as part from the Tsaobis Baboon Project, and all data were provided by Dr Guy Cowlishaw. My contributions to the dataset, during and prior to my PhD project, are detailed in Chapter four: Methods.

I have been provided invaluable advice and direction for the duration of this project for my supervisors. Dr Guy Cowlishaw and Prof Andy Fenton supported my conception of ideas, data collection. Additionally, they supported my plans for statistical analysis and writing of this thesis, alongside Dr Xav Harrison.

Chapter 6

Social network data and R code for calculating social network position were provided by Dr Alecia Carter.

Chapter 7

MHC data, including Supertype classifications, were provided by Dr Elise Huchard.