GASTROINTESTINAL PARASITE INFECTIONS IN CHACMA BABOONS (*Papio ursinus*) OF THE CAPE PENINSULA, SOUTH AFRICA:

the influence of individual, group, and anthropogenic factors

By

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Gastrointestinal parasite infections in chacma baboons (*Papio ursinus*) of the Cape Peninsula, South Africa: the influence of individual, group, and anthropogenic factors

DAMIANA F. C. RAVASI, July 2009

ABSTRACT

Habitat disturbance can lead to the alteration of host-parasite dynamics and ultimately influence the mechanisms that regulate wildlife populations. This study investigates whether anthropogenic changes in the Cape Peninsula, South Africa, have affected gastrointestinal parasite infections in a free-living population of chacma baboons (*Papio ursinus*). Data on parasite diversity and prevalence were obtained from 616 faecal samples collected from over 350 individuals in eight troops (six from the Cape Peninsula, one from Pringle Bay, and one from Wildcliff Nature Reserve) between July 2006 and August 2007. Faeces were processed using a modified formalin-ether sedimentation technique and helminth eggs and protozoan cysts were identified. The helminth and protozoan fauna of the Cape Peninsula baboon population was similar to both neighbouring and geographically disparate chacma baboon populations in South Africa.

Distribution of helminth infection within a troop was influenced by the age of the host but not by other individual-level traits (i.e., gender and female reproductive and social status). Protozoan and helminth species richness was highest in the troop (Kanonkop) with the least human contact and the most pristine indigenous vegetation and was lowest in the troop (Tokai) with the highest levels of anthropogenic disturbance. Prevalences of the nematodes *Trichuris* sp. and *Oesophagostomum* sp. were highest in the troop (Da Gama Park) with the most frequent human interactions. A series of potential host-intrinsic (e.g., host sex and age) and host-extrinsic (e.g., troop characteristics, climate) determinants of host-parasite dynamics were investigated but failed to explain the observed inter-troop variations in parasite infections. Molecular analyses of the ubiquitous and highly prevalent nematode, *Trichuris* sp., provided evidence of two genetically distinct *Trichuris* species, including a newly identified baboon parasite, named *T. papionis*, and another that strongly resembles (91% similarity between ITS1-5.8S rDNA-ITS2 sequences) the human *T. trichiura*. The latter finding provides the first evidence of a likely reverse zoonotic infection of baboons with human parasites and provides management authorities with a strong motivation to restrict the spatial overlap between the humans and baboons in the Cape Peninsula and indeed other regions of the Western Cape.

Keywords: *Papio ursinus* - chacma baboon - parasites - urbanization - *Trichuris* - molecular

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CHAPTER ONE

INTRODUCTION

Human activities have caused substantial and potentially irreversible changes to nonhuman primate habitats over the last century (Chapman & Peres 2001). One of the consequences is that nonhuman primates are increasingly forced to live in anthropogenically disturbed habitat mosaics of farmland, human settlements, forest fragments, and isolated protected areas (Chapman *et al.* 2006a). The Cape Peninsula in South Africa is a classic example of this phenomenon, with urban sprawl and agriculture posing a serious threat to the continued survival of the local chacma baboon (*Papio ursinus*) population. Historically baboons occurred throughout the peninsula, but they are currently restricted to 17% of the total land area (Kansky & Gaynor 2000). This loss of habitat has resulted in a dramatic drop in population numbers, with whole troops having been eliminated in many areas. At present there are only about 380 individuals distributed within thirteen troops on the peninsula (Beamish unpubl. data). The Cape peninsula baboons have effectively been forced into ever-closer contact with humans and this has resulted in a range of negative consequences for both parties. The baboons frequently sleep in and around urban areas and profit from the large volumes of human refuse discharged into their immediate environment. They have also become adept at raiding houses for food. In addition to living in close contact with the local population, baboons in the Cape of Good Hope section of the Table Mountain National Park have been inadvertently encouraged to come into close contact with overseas visitors, due to the expansion of inappropriate tourism developments, such as restaurants, takeaways, and picnic sites. In January 2006, the first serious attack by a baboon on a human raised the ire of the local population with many calls for the eradication of whole troops.

Habitat disturbance by humans can lead to health issues in wildlife that are still poorly understood, such as the alteration of host-parasite dynamics. This is one of the reasons why parasitic infections have been identified as a critical component to consider in conservation biology (May 1988; Scott 1988). Even if little is known about factors that influence the host range of parasites in natural populations (Pedersen *et al.* 2005), the impact of parasitic infections on the density and distribution of animal populations has been recognized as an important factor to be considered (Anderson 1979; Gulland 1992; Gregory & Hudson 2000; Hochachka & Dhondt 2000). Although helminth infections at low intensity are more common in nature, they have the potential to regulate host population abundance through density-dependent effects on either host survival or reproduction (Anderson & May 1978; Anderson & May 1979; May & Anderson 1979). In some studies, helminths have been found in all of the individuals of a group but no adverse effects of such high prevalence have been discernable (e.g., Ashford *et al.* 1990; Stuart *et al.* 1990). However, helminthic and protozoan parasites can affect host survival and reproduction indirectly by compromising host condition (Chandra & Newberne 1977; Boyce 1990; Coop & Holmes 1996). Important host functions such as nutrition, travel, predator escape, and competition for resources and mates can be impaired (Dobson & Hudson 1992; Hudson *et al.* 1992; Packer *et al.* 2003). Effects on the host due to severe parasitosis can also be more direct and include blood loss, tissue damage, castration, and even death (Chandra & Newberne 1977; Despommier *et al.* 1995). Anthropogenic changes to the habitat may result in the alteration of parasite transmission rates, host range, and virulence (Daszak *et al.* 2000; Patz *et al.* 2000).

It is currently unclear what aspects of anthropogenic changes to the physical environment facilitate the transmission of infectious agents among wild nonhuman primates or between nonhuman primates and humans. Recent investigations in Uganda have however demonstrated unequivocally that various forms of anthropogenic disturbance, such as logging and forest fragmentation, alter the dynamics of parasite infection in primate populations (Chapman *et al.* 2005a; Gillespie *et al.* 2005a; Chapman *et al.* 2006a; Gillespie & Chapman 2006). Prevalence of the nematode *Oesophagostomum* sp., a potentially debilitating parasite, was found to be higher among edge-dwelling red colobus (*Piliocolobus tephrosceles*) populations than in populations of the same primate species inhabiting the forest interior (Chapman *et al.* 2006a). The proportion of individuals with multiple infections was also greater at the edge and, in light of these results, it was speculated that interactions with humans could be linked to the observed patterns of infection (Chapman *et al.* 2006a).

Evidence that some conservation actions may actually endanger primate populations by promoting disease transmission is also alarming. As conservation agencies in Africa increasingly turn to ecotourism as a strategy to provide local communities with benefits from protected areas (Struhsaker *et al.* 2005), and as the number of research sites increases, so does the possibility of disease transmission via these activities (Eilenberger 1997). Already, a number of cases have been documented of primates in ecotourism and/or research sites contracting infections with likely human origins. For example, in 1996, a severe skin disease was documented among gorillas (*Gorilla gorilla*) at Bwindi Impenetrable National Park, Uganda, and skin biopsy confirmed the presence of scabies, a burrowing mite common to humans (Wallis & Lee 1999).

The rapid expansion of urban areas in countries inhabited by primates reduces their habitat but also introduces new easily accessible sources of food, such as city dumps, that can attract opportunistic species like baboons. Even if direct contact between human population and baboons might not happen, transmission of parasites such as helminths and protozoa can occur through contact with soil and water contaminated with the infectious stages of these parasites. In a study on intestinal parasites of baboons (*Papio hamadryas*) in Saudi Arabia, Ghandour (*et al.* 1995) found that groups of the primates that lived in areas with regular human contact presented higher parasite prevalences than groups with minimal human contact. It is possible that baboons have acquired certain human parasites species due to close contact with humans, maintain these parasites, and could thus act as reservoir hosts for the subsequent infection of humans (Nelson 1965; Nasher 1988).

Understanding the interactions between alteration of natural habitats and patterns of disease transmission is important to better develop conservation strategies. It is therefore important to understand how patterns of parasitism in wild hosts are influenced by host-intrinsic factors, (e.g., ranging patterns, Vitone *et al.* 2004; group size, Côté & Poulin 1995; and host density, Morand & Poulin 1998, Nunn *et al.* 2003), intraspecific and interspecific contact rates (Nunn *et al.* 2003), and diet (Eley *et al.* 1989), and environmental factors (e. g. climate, vegetation type, Huffman *et al.* 1997, Müller 2007). Studies on a variety of species have demonstrated that these factors can be affected by changes in habitat structure (Olupot *et al.* 1994; Heydon & Bulloh 1997; Patriquin & Barclay 2003). For example, primates that raid agricultural crops may develop decreased intensities of parasitism (Eley *et al.* 1989), since the improved nutrition may facilitate a more effective immune response. Hahn *et al.* (2003) found that some spirurid nematodes had increased prevalence in baboon (*Papio anubis*) groups that supplemented their nutrition by feeding on refuse, while others had decreased prevalence. On the other hand, since nonhuman primates and humans are susceptible to many of the same generalist parasites (Chapman *et al.* 2006a), monkeys ranging along forest edges may have increased parasitism stemming from frequent contact with humans.

The parasite fauna of baboons in different localities of Africa, including South Africa, has been well documented (e.g., Kuntz & Myers 1966; Goldsmid 1974; Meade 1984; Pettifer 1984; Eley *et al*. 1989; Appleton *et al*. 1991; Müller-Graf *et al*. 1996; Hahn *et al*. 2003; Hope *et al*. 2004; Legesse & Erko 2004). However, only a few studies addressed the potential role of human encroachment on the prevalence and diversity in baboon parasites (Appleton & Henzi 1993; Ghandour *et al.* 1995). The primary aims of this study are: 1) to provide the first data on the gastrointestinal parasite diversity of the geographically isolated and fragmented population of chacma baboons (*Papio ursinus*) ranging in the Cape Peninsula, 2) to compare these data with neighbouring populations and other studies in other parts of South Africa and Africa, and 3) to provide a detailed investigation into the potential role of host-intrinsic traits for parasite species richness and prevalences.

The risk of infection to primates living in fragmented landscapes is increased by a range of factors. These include a decrease in availability of adequate nutritional resources, reduction of home-range size, and constant reuse of terrestrial pathways, coupled to contamination from proximity of humans and domestic animals such as cattle, horses, and dogs. Such risks may have important negative consequences to the general health and growth potential of the Cape Peninsula baboon population. This study will also attempt to show how parasite infection dynamics are being affected by anthropogenic variables including urbanization, human interaction, and habitat disturbance. Finally, I hope to determine whether nematode species with a high prevalence (i.e., *Trichuris* sp.) in both the baboon and human Peninsula population are the result of cross-contamination between baboons and humans. To achieve this I will use genetic markers for the specific identification of parasitic nematodes to compare the sequences of human and baboon *Trichuris* spp.

This study could potentially contribute to our understanding of how urban and agricultural land transformation affects the dynamics of host-parasites in a primate population. From a conservation perspective, the threat to the baboon population of the Cape Peninsula has been acknowledged by conferring protected species status on them, but no firm management policies have yet been implemented because of a lack of fundamental research. While the baboons are protected by law from persecution, their habitat is being rapidly transformed into urban estates with no consequence given to the downstream effects of increased contact between baboons and humans. We still lack an understanding of the basic demographics of the population and the potential carrying capacity of the wilderness areas available to them.

Although the role of episodic outbreaks of infectious diseases on the risk of extinction for the population has been briefly discussed by Kansky and Gaynor (2000), no studies have been undertaken to assess the role of human interaction on host-parasite relationship in these baboons. If this study successfully demonstrates a clear link between parasite prevalence and proximity of baboons and humans then it provides conservation authorities and town planners alike with the necessary information to restrict overlap between the two populations.

Chapters 2 and 3 provide a detailed literature review and the methodology used in the thesis, respectively. Chapters 4 to 7 provide the results. Chapter 4 describes the parasite diversity and prevalence found in the Cape Peninsula baboon population and compares it to parasite infections in other locations of South Africa and Africa. In Chapter 5, host-intrinsic factors potentially affecting parasite infection are investigated in three study troops with known individuals. Parasite diversity and prevalences are compared across six Peninsula troops in Chapter 6, and both troop attributes and abiotic factors are estimated to investigate the potential ecological attributes that may affect parasite infection rates between troops. Finally, in Chapter 7, the nematode *Trichuris* infecting the study baboon population is analyzed with molecular tools and compared to the whipworm (*T. trichiura*) found in humans, to investigate possible cross-transmission of the helminth between the two primate species.

CHAPTER TWO

LITERATURE REVIEW

2.1 Host-parasite dynamics

2.1.1 Impact of parasitic infections

Infectious diseases and parasites are a common component of animal populations (Hudson *et al*. 1998; Swinton *et al*. 1998; Begon *et al*. 1999). Similar to predation and resource limitation, parasites are also likely to play a part in constraining the growth of natural animal populations (May & Anderson 1978, 1979; Anderson & May 1979; Anderson 1980). The average mammal may harbour a multispecies community of several hundred individual macroparasites (Dobson *et al*. 1992). For example, feral Soay sheep (*Ovis aries*) on the island of St. Kilda, Scotland, harbour more than 15 different species of helminths alone (Gulland 1992).

Although low intensity infections of helminths are more common, these parasites have the potential to regulate host population abundance through density-dependent effects on either host survival or reproduction (Anderson & May 1978). Gulland (1992) suggests that parasites contribute to mortality in malnourished hosts, exacerbating the effects of food shortage. Parasites may indirectly affect host survival by increasing the susceptibility of the infected host to predation or by reducing the competitive fitness of the infected host (Scott 1988). Effects on host reproduction can be direct (castration and consequent reduction of reproductive success) and indirect (delayed growth, delayed age at sexual maturity, decreased reproductive lifespan, abortions, and reduced ability to rear offspring) (Scott 1988). For these reasons, parasitic helminths can be considered as supremely adapted predators that constantly impose a slow but steady drain on host resources, and thus significantly influence their hosts' energetic functions, behaviour, demography, and evolution (Dobson *et al*. 1992).

Moreover, parasites have been linked increasingly with dramatic local and global declines of wildlife species, including lions, black-footed ferrets, Hawaiian forest birds, and many amphibian species (e.g., Dobson & Grenfell 1995; Packer *et al*. 1999; Daszak *et al*. 2000; Bermejo *et al.* 2006). Brain and Bohrman (1992) found that chacma baboons (*Papio ursinus*) living in the Namib Desert were heavily infected by ticks and speculated that these infections were responsible for more than half (*n*=18) of recorded infant deaths.

In conclusion, parasites may play an important role in population and community regulation, and might correspondingly be important in conservation biology (Dobson & Hudson 1986; May 1988; Scott 1988; Morand & Poulin 1998). Understanding the factors that underlie patterns of parasite diversity is vital to identifying ecological principles governing biodiversity. Ecological studies may allow prediction of the combination of parasite, host, and environmental parameters most likely to lead to disease emergence (Daszak *et al*. 2000).

2.1.2 Factors affecting host-parasite dynamics

The study of factors determining the composition and structure of natural communities has always been at the core of ecology. This is also true, but only recently, for parasite communities (Poulin 1995). Many factors have been proposed to account for patterns of parasite species richness (PSR). Environmental conditions affect the viability and behaviour of parasite propagules (Rogers & Sommerville 1963). A growing number of comparative studies (e.g., Davies *et al*. 1991; Poulin 1995; Gregory *et al*. 1996; Morand & Poulin 1998; Arneberg 2001) have demonstrated links between parasite diversity and both host- (e.g., body size or group size) and population-level traits (e.g., density). Other ecological traits commonly thought to influence or be correlated with local parasite community richness (parasites in the whole host population) are host age, sex, diet, habitat, seasonal variations, and mean number of parasite individuals per host (Kuris *et al*. 1980; Price & Clancy 1983; Bush *et al*. 1990; Esch *et al*. 1990; Bell & Burt 1991; Sousa 1994). Following transmission, successful establishment and reproduction of the parasite are affected by the internal conditions of the host for example, gut physiology, existing infection(s), and immune response.

2.1.3 Anthropogenic disturbance and host-parasite dynamics

Human activities, which are ultimately responsible for the majority of conservation problems, can interact with disease agents (May 1988). Anthropogenic changes to the habitat may result in the alteration of parasite transmission rates, host range, and virulence (Daszak *et al.* 2000; Patz *et al.* 2000). Together these changes may pose a significant conservation risk to nonhuman primate populations (Wallis & Lee 1999).

Recent investigations in Uganda have demonstrated that various forms of anthropogenic disturbance alter the dynamics of parasite infection in primate populations (Chapman *et al.* 2005a). Among red-tail guenons (*Cercopithecus ascanius*), for example, the prevalence and richness of gastrointestinal parasite infections were greater in logged than in undisturbed forest (Gillespie *et al*. 2005a). Black-and-white (*Colobus guereza*) and red colobus (*Piliocolobus tephrosceles*) in forest fragments had increased parasite prevalence compared with populations in undisturbed forest (Gillespie & Chapman 2006) and infection levels were strongly influenced by host density (Chapman *et al*. 2006a). Finally, a study comparing parasite infection among colobus populations living at the forest edge and in the interior found that the proportion of individuals with multiple infections was greater at the edge (Chapman *et al*. 2006a) and the prevalence of specific parasites varied between groups. For example, *Oesophagostomum* sp., a potentially debilitating parasite, was 7.4 times more prevalent among edge-dwelling red colobus than in animals inhabiting the forest interior.

Identifying general principles governing parasite occurrence is critical for managing vulnerable wildlife populations and mitigating risks to human health. However, ecological data on parasites of important host species is still lacking (Marathe *et al.* 2002). It is currently unclear what aspects of anthropogenic changes to the physical environment facilitate the transmission of infectious agents among wild nonhuman primates or between nonhuman primates and humans. However, to better develop conservation strategies to deal with established and changing patterns of disease, we must understand the interplay between the alteration of ecosystems and disease transmission probabilities.

2.2 Studies on parasites of wild baboons in Africa

The gastrointestinal parasites of baboons in Africa have been documented in a number of studies. The first studies comprised broad-scale surveys and were conducted in East Africa (Myers & Kuntz 1965; Kuntz & Myers 1966; Kuntz & Myers 1967; Myers *et al*. 1970; Kuntz & Moore 1973) and southern Africa (Tadros 1966; Myers *et al*. 1971; Goldsmid 1974; McConnell *et al*. 1974; Goldsmid & Rogers 1978; Pettifer 1984). These early studies stressed the value of baboons as models for medical research and gave mainly descriptive accounts of the parasites found.

Subsequent studies emphasized PSR and prevalence in baboons in different geographical localities (Hausfater & Watson 1976; Pettifer 1984; Appleton & Henzi 1990; Appleton *et al*. 1991) and under different ecological environments (Meade 1984; Eley *et al*. 1989; Appleton & Brain 1995). Meade (1984) moved further than compiling checklists of parasite species and explored the determinants of host-parasite relationships. In some studies, baboons were trapped to obtain samples (Eley *et al*. 1989; Munene *et al*. 1998). However, in many cases, the methodology was non-invasive and the animals were not handled in any way. This approach allowed repeated sampling of individuals over time, and the investigation of the effects of the hosts' social status, reproductive condition, season, and food and water availability on the host-parasite relationship (Hausfater & Sutherland 1984; Meade 1984). More recent studies have investigated the role of genetic factors in levels of parasite infection in different baboon troops (Müller-Graf *et al.* 1996). However, only a few studies have addressed the potential role of human encroachment on the prevalence and diversity in baboon parasites (Appleton & Henzi 1993; Ghandour *et al*. 1995). Baboons are opportunistic feeders, readily raid crops and range into human habitats. Their potential role in the maintenance and spread of zoonotic parasites and the resultant concern for human welfare has lead to a fair number of research articles on their parasites (Appleton 1989; Ghandour *et al*. 1995; Zahed *et al.* 1996; Munene *et al*. 1998; Muriuki *et al*. 1998; Erko *et al*. 2001; Hahn *et al*. 2003; Mutani *et al*. 2003; Hope *et al*. 2004; Legesse & Erko 2004). Appendix A summarizes the diversity and prevalence of gastrointestinal protozoa and helminths found in *Papio ursinus* and other species of baboons at different localities within Africa.

2.3 Factors influencing parasite infection

Important factors potentially influencing mechanisms of parasite infection in primates are presented schematically in Figure 2.1. Host-intrinsic and host-extrinsic (habitat, parasite) factors can be influenced in several ways by the presence of humans and their activities, as shown by the arrows in Figure 2.1. The chapter titles are in bold if they describe factors influenced by anthropogenic activities. In the same way, the chapter titles underlined highlight factors investigated in this study.

2.3.1 Host-individual level

Intra-individual variation

Temporal variability in parasite stage output in a host may be very high (Anderson & Schad 1985). This variation could be due in part to the ecology of the parasite: egg production depends on the number of female worms living in the host individual; other stages (i.e., larvae, prepatent adults, adult males) could be present in the host, without releasing eggs (Anderson & Schad 1985; Warnick 1992; Cabaret *et al.* 1998). Parasites may also vary in how they release eggs; some species might release eggs or larvae intermittently while others may release eggs continuously (Anderson & Schad 1985). Such differences may translate into high variation in the number of parasite stages within a particular scat sample and across different scats ultimately leading to high variation in prevalence estimates (Müller 2007).

Age and sex

In humans, children are known to have a higher infection probability from soil-transmitted parasites than adults, due to their higher contact with infected soil when playing outdoors (Bundy 1988). In the case of nonhuman primates and other animal species, potential effects of age on parasite infections would be due to other behavioural traits, since all ages have the same degree of contact with soil. According to Scott (1988), many parasites are common in young animals and remain prevalent throughout their lifespan, whereas other parasites are common in young animals, but decrease in prevalence and intensity in older animals. Dobson *et al*. (1992) concluded that both the diversity of parasite species and the burden of each species tend to increase with host age.

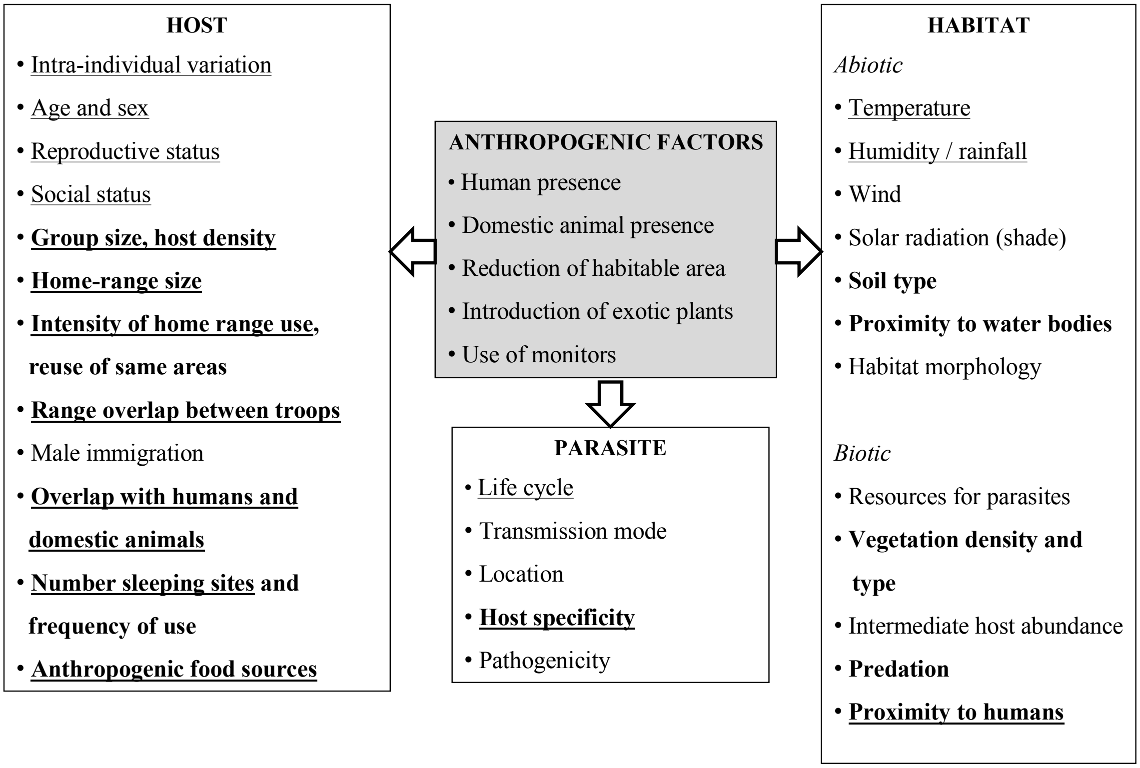


Figure 2.1 Host, habitat, and parasite factors potentially influencing mechanisms of parasite infection in primates. Factors in bold are influenced by anthropogenic activities. Factors underlined are investigated in this study.

Investigations of helminth infection probability in different primate species have led to contradictory results. Mutani *et al*. (2003) and Gillespie *et al*. (2005b) did not find any significant difference in prevalence according to age in Barbados green monkeys (*Cercopithecus aethiops sabaeus*) and three colobus species, respectively. By contrast, infant gorillas exhibited higher parasite infestation (helminth eggs per gram and protozoa per gram) than juvenile and adult gorillas for various parasites (Eilenberger 1997; Lilly *et al*. 2002). The effects of age on parasite infection have also been examined in a number of field studies on baboons. In olive baboons (*Papio anubis*), Miller (1960) discovered higher levels of schistosome infections in adult males than in immature males, while females showed no age-related pattern. Hausfater and Watson (1976) found that adult males of yellow baboons (*Papio cynocephalus*) shed more eggs of intestinal parasites than subadult males. These patterns could have also been linked to differences in social status between mature and immature males. Two studies on baboons (Meade 1984; Müller-Graf *et al*. 1996) found a negative association between *Strongyloides* prevalence and individual age. It has been suggested that this could be due to the fact that *Strongyloides* is transmitted vertically to infants from their mothers, and partial immunity then develops, persisting into adulthood. Moreover, the immune response of infants is generally weak (Nunn & Altizer 2006). No other helminth showed an association with age in the study by Müller-Graf *et al*. (1996). Meade (1984) reported that most of the other parasites analyzed showed a trend to increase with age, the opposite trend to *Strongyloides*. Looking at these examples on the whole, it is possible to expect in general a positive association between parasite diversity and intensity, and individual age, as a consequence of parasite accumulation over time (Bell & Burt 1991; Dobson *et al.* 1992; Morand & Harvey 2000; Nunn & Altizer 2006).

The larger body size of male baboons has been suggested to be a possible cause of differences in patterns of soil-transmitted parasites between males and females (Nunn & Altizer 2006). A larger body size has been suggested to necessitate higher food consumption rates and consequently higher exposure to more infectious stages of parasites. The larger nutritional requirements of males would possibly also increase their general susceptibility to infections (Barrett & Henzi 1998). Pregnant and lactating females would also be predicted to show increased consumption rates, suggesting that parasite levels may be further linked to reproductive status (see next section). Other sex differences in the body structure include hormones, which could also lead to differences in parasite infection. Again, pregnant females may differ from anoestrus females through the effects of hormonal changes on the immune response (Solomon 1969; Alexander & Stimson 1988), whilst in males testosterone may have immunosuppressive effects (Folstad & Karter 1992; Zuk & McKean 1996).

In general, male hosts have been found to be more susceptible than females to parasitic infections (Besch 1964; Berg & Beck 1968; Mankau & Hamilton 1972). A comparative study on mammals (Moore & Wilson 2002) has concluded that males showed higher parasite prevalence than females. However, analyses on different primate species, including gorillas (Eilenberger 1997), Barbados green monkeys (Mutani *et al*. 2003), and colobus monkeys (Gillespie *et al*. 2005b) suggest that sex does not have a significant impact on parasite prevalences. Furthermore, Gillespie *et al*. (2004) did not observe any difference in parasite prevalence between male and female redtail guenons (*Cercopithecus ascanius*), except that only females harboured *Oesophagostomum* sp. and *Strongyloides fuelleborni*.

In baboons, few studies found a correlation between sex and parasite prevalence: Hausfater and Watson (1976) reported higher abundance of eggs of the nematodes *Trichuris* sp. and *Trichostrongylus* sp. in yellow baboon females. Pettifer (1984) reported higher prevalence of *Physaloptera caucasica* in chacma baboon males, while Meade (1984) found a higher prevalence of the same parasite in adult females. Meade (1984) suggested that the latter finding could be due to sex differences in the consumption of the arthropod intermediate hosts. Müller-Graf *et al*. (1996) found a higher intensity of infections in olive baboon females by an indirectly transmitted nematode, *Streptopharagus* sp. In a later study, Müller-Graf *et al*. (1996) found a higher prevalence of *Schistosoma mansoni*, a trematode transmitted through snails, in male baboons, and suggested that this was due to the fact that males more frequently contacted water containing infectious stages of this helminth. In summary, despite there being relatively few consistent patterns with respect to the sex of a primate and parasite diversity and prevalence it is still predicted that on average males will have higher parasite infection than females, because of the combination of higher stress levels and greater exposure to parasites as a consequence of their behavioural differences (Meade 1984; Nunn & Altizer 2006).

<u>*Reproductive status*</u>

Patterns of reproduction are aseasonal in chacma baboons (Estes 1991) and births occur throughout the year in the Cape Peninsula troops (personal observation). This means that, unlike many other animal species, variations in parasite infections due to the reproductive cycle would not be confounded by seasonal variations. Courtship displays, mate competition, gestation, parturition, and lactation may cause energetic and social stress that could negatively affect the immune system and therefore increase parasite infection indices like prevalence and intensity (Klein & Nelson 1999; Bercovitch & Ziegler 2002). It has been shown that mammals decrease their own immune functions during gestation and birth (Lloyd 1983), possibly to reduce harm to the foetus. Higher energy demands during pregnancy and lactation could force an individual to forage more and consequently increase the risk of infection with soil-transmitted parasites. However, the effects of higher infection risk could be masked by the short span of the reproductive cycles (about 2 years between the start of pregnancy and the end of lactation) in comparison to the longer life span of worms of one to several years (Brack 1987).

Reproductive status in baboons has been related to helminth ova output but results are not consistent across studies. Hausfater and Watson (1976) showed that ova emission in yellow baboon females in Amboseli decreased from sexually cycling females to anoestrous and, finally, pregnant females. By contrast, Meade (1984) in the same Amboseli population observed the highest rates of ova emission among pregnant females. Cycling females still had higher output than lactating ones, but swelling females had lower output than anoestrus females. Müller-Graf *et al*. (1996, 1997) found that *Trichuris* sp. intensity of infection was higher in lactating baboon females at Gombe, while pregnant females showed the lowest intensity of infection. Clearly, prevalence does not show any consistent association with the baboons' reproductive status across different studies. Hausfater and Sutherland (1984) recorded a very sharp rise in helminth egg production immediately after female baboons gave birth and correlated it to the rapid change in the female's progesterone levels. This reproductive strategy might facilitate an early assault on newborn infants by the parasite. One parasite species, *Strongyloides fuelleborni*, is acquired by infants while still in the womb. In conclusion, the few data that are available provide contradictory results and make it difficult to build any clear predictions based on the reproductive cycle of females. It is however expected that parasite intensity (i.e., the number of adult individuals of a particular taxon infecting an individual host (Margolis *et al.* 1982)) and egg output would be higher during the more energetically expensive phases of pregnancy and lactation.

Social status

Variations in social rank between individuals in a group could lead to different levels of parasite infection through various mechanisms. Thus, lower-ranking individuals could be forced to use habitats of lower quality that might contain more parasites (Nunn & Altizer 2006) while higher-ranking individuals may be more susceptible to infection due to the immunosuppressive effects of elevated testosterone and cortisol that are associated with high rank (Folstad & Karter 1992; Dixson 1998; Bercovitch & Ziegler 2002). Alternatively, access to better food resources due to higher rank could improve the host condition and hence immunocompetence, leading to better defences against parasite infection and lower prevalence or intensity of infection (Nunn & Altizer 2006). In addition, low ranking animals may experience acute periods of high stress that might decrease the ability of the immune system to fight parasite infections (Lloyd 1995; Cohen 1999). Evidence from studies on primates is once again conflicting. Hausfater and Watson (1976), as well as Meade (1984) reported that dominant adult male yellow baboons had higher outputs of helminth eggs than subordinate males, while no correlation was detected among adult females of different rank. Muller-Graf *et al*. (1996) found no association between dominance rank and indices of helminth infection in olive baboons, while Eley *et al*. (1989) reported that lice were more common on low-ranking olive baboons.

Parasitism itself could have an effect on ranking, making heavily parasitized hosts less able to achieve high dominance rank (Nunn & Altizer 2006). However, this effect would only be apparent in male baboons as females typically inherit their rank from their mothers. In conclusion, the association between social rank and parasite infection risk in primates is not clear-cut but a positive correlation is predicted between dominance rank and indices of parasite infection.

2.3.2 Host-group level

Group size and host density

Consistent positive correlations between host group size and both the prevalence and intensity of contagious parasites were found by Côté and Poulin (1995) in a meta-analysis study. Host population density is considered to be of central importance to infection rates in directly transmitted parasites (Poulin 1998). However, parasite transmission mode must be carefully taken in consideration when investigating patterns of species richness and prevalence. In the case of parasites transmitted via contaminated soil or water, host density and group size should play a less important role, than in directly transmitted parasites (Côté & Poulin 1995; Altizer *et al*. 2003). However, it may also be argued that larger group size and higher host density could lead to higher levels of defecation and soil contamination, and therefore higher risk of indirect gastrointestinal parasite infections. Freeland (1979) found a positive association between group size and the number of intestinal protozoan species in mangabeys (*Cercocebus albigena*) at Kibale. A positive trend between nematode infections and group size was found by McGrew *et al*. (1989) in three groups of baboons at Gombe. However, comparative studies including tests of PSR using data on protozoa, helminths, and viruses have revealed only a few links between social group size and disease risk (Nunn *et al*. 2003; Vitone *et al*. 2004).

Within-species studies have demonstrated a positive correlation with parasite prevalence and diversity and the density of the host (Ghandour *et al*. 1995; Arneberg *et al*. 1998; Morand & Poulin 1998; Arneberg 2001; Nunn *et al*. 2003) although exceptions have been noted (Chapman *et al*. 2005c; Müller 2007; Vitazkova & Wade 2007). Higher host density could also increase parasite infection indirectly through nutritional stress resulting from higher competition for available food resources. Malnourished hosts are predicted to have lower immunological competence, which would result in a reduced ability to withstand infection (May & Anderson 1979).

Anthropogenic activities could have an influence on host density and, therefore, parasite infection through the reduction of suitable habitat area. Gillespie and Chapman (2006) demonstrated in a five-year study on colobus in Uganda that forest fragmentation altered prevalence and infection risk and that these factors were largely influenced by variation in host density (Chapman *et al.* 2005a).

In summary, I would predict a positive correlation between group size/host density and parasite diversity/prevalence in the Cape Peninsula baboons.

Home-range size and intensity of use; reuse of same areas

Utilization of large home ranges or longer routes travelled per day should translate into exposure to a greater variety of parasite species, resulting into higher parasite diversity (Watve & Sukumar 1995; Nunn *et al*. 2003; Vitone *et al*. 2004). Vitone *et al*. (2004) found a positive association between individual ranging behaviour and diversity of helminth parasites with complex life cycles (cestodes, trematodes, and acanthocephalans). It is also expected that hosts restricted to smaller home ranges would be more exposed to reinfection due to the accumulation of parasite infectious stages in the area used (Freeland 1976; Hausfater & Meade 1982; Côté & Poulin 1995). In a study on gorillas by Eilenberger (1997), the group with the most overlap with other groups' home ranges and shortest daily movement ranges was the most infested with parasites. It was also hypothesized that repeated utilization of an area after short intervals could result in higher parasite infestation.

Therefore, hosts with larger home ranges should harbour a higher number of parasite species, whereas hosts ranging in smaller home ranges should experience higher parasite prevalence and intensity of infection (Freeland 1976). Higher parasite prevalence and intensity of infection is also expected to correlate positively with higher intensity of use of the same areas in the home range. Anthropogenic activities might alter the home-range size of a group of primates and therefore have an influence on parasite diversity and prevalence of parasites.

It has been suggested that primates might be able to reduce their probability of parasite infection through the avoidance of habitats containing high densities of parasite infective stages (Freeland 1976, 1980). Gilbert (1997) found that red howling monkeys (*Alouatta seniculus*) moved to specific sites to defecate, free of underlying vegetation. This defecation behaviour decreases the likelihood of contaminating potential food sources or arboreal pathways and may therefore be an important parasite avoidance strategy. By contrast, Olupot *et al*. (1997) suggested that ranging patterns in mangabeys did not vary to reduce the risk of parasite infection through faecal contamination, but was rather driven by spatial variation in seasonal fruit availability. Baboons do not appear to have specific defecation sites, although Hausfater and Meade (1982) proposed that the temporal pattern of sleeping site alternation shown by baboons in Amboseli could reflect a behavioural strategy for avoidance of parasite infection through contaminated soil.

Range overlap between troops; *male immigration*

Freeland (1979) viewed primate social groups as biological islands. Protozoan fauna and parasitic prevalence are predicted to be much more similar within than between social groups. Freeland found intergroup differences in the composition of protozoan fauna in different animal species, except for *Papio anubis*. All groups of savannah *P. anubis* exhibited identical protozoan faunas, possibly because of the high rate of exchange of individuals between groups. Therefore, increased contact between social groups occurring through range overlapping is predicted to increase the probability of infection with water- or soil-transmitted parasites. Furthermore, the immigration of foreign conspecifics into a group of blue monkeys (*Cercopithecus mitis*) resulted in an increase in the species richness of the group's protozoan fauna (Freeland 1979). Thus, the general prediction is that most measures of disease risk will increase with range overlap and the frequency of immigration (Nunn & Altizer 2006).

Overlap with humans and domestic animals

Parasites introduced by humans and those that appear following the restriction of natural habitat can have a severe impact on free-ranging animals. Higher parasite prevalence in baboons was associated with close human contact by Ghandour *et al*. (1995) and Munene *et* *al*. (1998). Müller-Graf *et al.* (1997) found that the baboon troop with the most contact with people showed the highest prevalence of infection with *Schistosoma mansoni*. In a study by Nutter (unpubl. data) on chimpanzees (*Pan troglodytes schweinfurthii*) in Gombe, the community that had the most contact with humans had a higher number of parasite species and prevalence compared to those communities living at a greater distance from humans (in Wallis & Lee 1999). Rolland *et al*. (1985) examined three groups of baboons in Amboseli and found that the troop that entered into frequent contact with a human refuse area had a higher prevalence of antibiotic-resistant enteric bacteria than natural troops. However, certain studies did not find any parasites directly attributable to exposure to people and their activities (e.g., Hahn *et al*. 2003; garbage-feeding baboons).

Although cross-transmission between livestock, humans, and nonhuman primates has not been studied for most of the gastrointestinal parasites, available reports indicate some of them cross-infect different hosts in endemic areas of Africa (WHO 1979; Hira & Patel 1980; Soulsby 1982; Meade 1984; Appleton 1989; Muchemi 1992; Muller-Graf *et al*. 1997). Taylor *et al.* (2001) reported that 96% of the 287 helminth species found in humans are considered zoonotic. Baboons were suggested to be acting as reservoirs of *Schistosoma mansoni* in various localities, such as Ndala River, Tanzania (Fenwick 1969), Saudi Arabia (Zahed *et al.* 1996), and Ethiopia (Erko *et al*. 2001). Strongyles, which are important livestock parasites (Soulsby 1982), were among those found in the primates studied by Muriuki *et al*. (1998) with proven public health significance like cryptosporidiosis, giardiasis, amoebiasis, and strongyloidiasis (Acha & Szyfres 1989; Manson-Bahr & Bell 1989a,b). The latter parasites commonly infect dogs, cats, rodents, and livestock (Amyx *et al*. 1978; Soulsby 1982; Acha & Szyfres 1989), and are therefore readily transmitted through various environmental routes. Communal water holes (Hausfater & Sutherland 1984), human refuse, and food wastes, including animal parts (Rolland *et al*. 1985; Hahn *et al*. 2003), and soil (Muriuki *et al*. 1998) are all likely areas for cross-transmission of parasites. Parasite host specificity and cross-transmission between humans and nonhuman primates is treated in more detail in the section below on host specificity.

Three of the six Cape Peninsula baboon troops included in this study (Cape Point, Da Gama Park, and Tokai troops) were subjected to an invasive form of management, namely being herded by baboon monitors. The monitors are local people employed to herd the troops away from urban areas on a daily basis. The objective of the monitors is to reduce human-baboon conflict by preventing the baboons from raiding in urban areas. A direct consequence of herding is that baboons are forced into certain areas within their home range and their choice of sleeping sites is constrained (van Doorn unpubl. data). Frequent use of certain portions of the home range may result in a higher frequency of contact with faeces and hence increase the chances of parasite infections for all troop members (see section below on use of sleeping sites). Herding the baboons away from preferred feeding areas into areas that are frequently visited may also result in local depletion of food reserves, thus adversely affect the nutritional status of the monitored troops, and hence increase their susceptibility to infection (see below).

Number of sleeping sites; frequency of use

Sleeping sites may be one of the major sites of contact between primate hosts and both parasites and other pathogens (Freeland 1976, 1977). Hausfater and Meade (1982) demonstrated that parasite larvae were present at a higher density in the soil beneath baboon sleeping sites than in comparable microhabitats. In response to the higher risk of infection at sleeping sites, the baboons were observed to avoid prolonged periods of consecutive nights at a given sleeping site (Hausfater & Meade 1982). Hausfater and Sutherland (1984) noted that the baboons' own sleeping sites were the primary source of contact with their intestinal parasites while Meade (1984) observed that one or two nights' was usually sufficient to result in substantial faecal build-up beneath a grove and the study animals avoided groves during times of peak larval hatching. Intriguingly the mean return time to a grove by the baboons was very close to the number of estimated days necessary to reduce the probability of contacting infective stages of their parasites. It is possible that the proximate cue for this decision is the odour from the faeces that have accumulated beneath their sleeping sites. By contrast, Anderson and McGrew (1984) were not able to relate the build up of intestinal parasites in faeces below sleeping trees to their use in Guinea baboons (*Papio papio*).

Anthropogenic food sources

Host diet is expected to determine, at least partially, the number of parasite species to which a host will be exposed (Poulin 1995). Baboons are opportunistic and generalist in their diet. They are thus exposed to a wide number of infection sources and may therefore be expected to have high parasite diversity. Groups living in close contact with humans and foraging on garbage are potentially exposed to more sources of infection such as rotten food, infected meat, and human waste. Folivorous primates are known to reduce parasite intensity by the selective ingestion of plants with chemical or physical anti-parasitic properties (refer to Huffman (1997) and Huffman (2007) for a review on primate self-medication). The indigenous vegetation of the Cape Peninsula, fynbos, is rich in bitter tannins (Manning & Paterson-Jones 2008) and other secondary plant metabolites that are thought to possess anti-parasitic effects (Coop & Kyriazakis 2001). Permanent water sources could also play a role in parasite infection by offering ideal conditions for the development and transmission of parasites. Amboseli baboons were thought to limit their visits to drinking holes in part to avoid the moist soil that surrounds these holes (Meade 1984).

The nutritional state of the host is also likely to play an important role in parasite infections, with parasites amplifying the effects of low levels of nutrition (Anderson & May 1979). Studies in the laboratory (Keymer & Hiorns 1986; Munger & Karasov 1989) and in the field (Gulland 1992; Tocque 1993; Murray *et al*. 1998) suggest that vertebrate populations may be influenced by the interactive effects of food shortage and parasitism (Keymer & Hiorns 1986; Holmes 1995; Murray *et al*. 1998). Dietary stress may exacerbate the clinical consequences of parasitic infection through immunosuppression (Holmes 1995; Milton 1996). If this occurred, nutritional status and parasitism would have synergistic effects on the host, that is, the individual effects of each factor would be amplified when co-occurring.

Eley *et al*.'s (1989) hypothesis of a causal relationship between host nutrition and helminth parasite infection was supported by her findings in two baboon troops. The provisioned troop (human refuse) had access to abundant food and had lower prevalence levels of the helminth strongyles than the non-provisioned troop. In other studies on baboons, a high prevalence of helminths was associated with terrestrial feeding behaviour (Munene *et al*. 1998), which, in one case, resulted from winter (dry) food shortage (Appleton & Henzi 1993).

2.3.3 Abiotic habitat factors

Temperature, humidity, and seasonality

Climate and seasons are expected to influence host-parasite dynamics through direct effects on food, water, and ranging patterns, and indirectly through influences on the survival of the infective and free-living stages of their parasites and on the availability of certain invertebrate intermediate hosts for the parasites (Meade 1984). Different species of nematodes are more or less susceptible to different microclimatic conditions at different stages of their life cycles (Gordon 1948; Smith 1990). For example, eggs of the genus *Trichuris* seem particularly able to survive under conditions of extreme cold (Rogers & Sommerville 1963).

Moisture appears to be a critical factor to parasite survival and the survival of eggs at any particular temperature correlates positively with humidity (Rogers & Sommerville 1963). Hausfater and Meade (1982) found that baboons avoided contaminated sleeping sites more often in the rainy season than in the dry season. Other studies of arboreal primates have shown a positive relationship between moist environments and intestinal macroparasite infections (Stuart *et al*. 1993, 1998; Stuart & Strier 1995; Stoner 1996). McGrew *et al*. (1989) found higher nematode prevalence and intensity in baboons and chimpanzees at Gombe, compared to populations ranging at Mt Assirik, a location with drier conditions. Montane baboon troops in South Africa were found to harbour less parasite species than lowland troops with higher humidity (Appleton & Henzi 1993). In Saudi Arabia, mild and cool climatic conditions favoured high prevalence of parasites in baboons, while prevalence was very low in hot and dry conditions (Ghandour *et al*. 1995). The extreme abiotic conditions of soil and water found in the Namibian desert resulted in a protozoan-dominated parasite fauna (with direct life cycle) in baboons. Elsewhere in the same country, a helminth-dominated fauna was found under more moderate climatic conditions (Appleton & Brain 1995). In the Cape Peninsula, the climate is predicted to become hotter, drier, and windier in the near future (Mukheibir & Ziervogel 2007). These conditions could have a negative impact on the survival of helminth infectious stages, and thus lead to decreased parasite infection in baboons and to a protozoan-dominated parasite fauna similar to that found in Namibian baboons.

Seasonality may therefore also be expected to play a role in parasite development and infection. Huffman *et al*. (1997) found that the prevalence of infection by the nematode *Oesophagostomum stephanosomum* in chimpanzees increased during the wet season, while the nematodes *Trichuris trichiura* and *Strongyloides fuelleborni* showed no seasonal variation in the same population. In a more recent study, Huffman *et al.* (2009) found significantly higher *Oesophagostomum stephanosomum* prevalence in chimpanzees at Budongo (Uganda) during the wet months, while no seasonal difference in *O. stephanosomum* prevalence in chimpanzees was noted at Mahale (Tanzania). For *Strongyloides fuelleborni* and *Trichuris trichiura*, the prevalence did not change between the same sites over different seasons, suggesting that within-site variation in rainfall patterns had little influence on prevalence.

However, inter-site differences in the distribution of rainfall seemed to explain the inter-site significant differences in the prevalence of *Strongyloides fuelleborni* and *Trichuris trichiura*. Spirurid nematode prevalence increased in the dry season in Amboseli baboons (Meade 1984). By contrast, prevalences of the worms *Bertiella studeri* and *Oesophagostomum bifurcum* in chacma baboons were higher during the wet season (Pettifer 1984), while the nematode *Trichostrongylus falculatus* was more common in the dry season. Gillespie *et al*. (2005b) found no correlation between parasite prevalence and rainfall in colobus monkeys and guenons (Gillespie *et al*. 2004). Seasonal effects could be masked by the simple fact that parasites typically live longer than a season and thus produce eggs year-round, effectively masking any potential difference in host susceptibility to infection in different seasons that may be due to climatic variation.

Wind

Wind could play an important role in the dispersal of parasite infectious stages, particularly helminth eggs, and protozoan oocysts. Strong persistent winds are a characteristic of the Cape Peninsula summer season. Adams *et al*. (unpubl. data) revealed that *Trichuris* sp. eggs were readily dispersed by the wind in the Cape Peninsula and suggested that this was a likely source of infection for communities removed from direct sources of the parasite.

Soil type

Soil type has an important influence on the survival of infectious stages of parasites (Rogers & Sommerville 1963). In particular, soil texture influences the active movement of parasitic stages, and therefore their ability to move into deeper soil layers where they can find protection from adverse environmental conditions (Storey & Phillips 1985; Mizgajaska 1993; Saathoff *et al*. 2005b). Most importantly, soil type affects soil moisture. Predictions and conclusions for the effects of different soil types on parasite infectious stages are contradictory. For example, Saathoff *et al.* (2005a) found in the literature that *Ascaris* sp. infections are more common on clayey soil than on sandy soil (in sandy soils helminth eggs are washed more quickly to lower soil strata where they are unavailable for infection). Rogers and Sommerville (1963) had demonstrated that *Ascaris* sp. eggs could survive for long periods in clay or loam soils, even in the absence of shade, but that they perished rapidly in sandy soils. However, Saathoff *et al.* (2005a) did not find epidemiological evidence in the literature to support this claim and did not find any clear pattern in their study either. The same authors, in a later study (Saathoff *et al.* 2005b), demonstrated the negative effect of clay on hookworm larvae. In contrast, sandy soils were proven to have affected positively the development and transmission of hookworm larvae. The Cape Peninsula is characterised by sandy, acidic soils, which may promote or adversely affect the development and survival of parasite stages. There are also areas with large amounts of clay present in the soil and it will be of interest to investigate differences in egg survival in these different soil types in the Peninsula.

Proximity to water bodies

As already mentioned in the previous section on diet, permanent water sources offer ideal conditions for the development and transmission of parasites and could play a role in parasite infection. They also represent a potential point of encounter between baboons and other wildlife and humans, increasing the probabilities of parasite cross-transmission between different host species. For example, Fenwick (1969) suggested that humans bathing in Ndala River in Tanzania were contracting *Schistosoma mansoni* from the baboons acting as reservoir hosts in the area; the river was the point where cross-transmission occurred.

2.3.4 Biotic habitat factors

Vegetation density and type

Vegetation type and density will influence soil moisture and hence parasite survival probability. Vegetation type will also influence the production of leaf litter and dead wood, which could favour the survival and development of parasite stages by decreasing fluctuations in soil humidity and temperature (Sayer 2006). Parasite diversity and prevalence would then be expected to correlate positively with abundance of leaf litter and deadwood in the host's environment (Müller 2007).

In the Cape Peninsula, exotic vegetation has greatly increased the total biomass of plants resulting in substantially higher leaf litter and dead wood. Thus, exotic vegetation may increase the soil moisture and provide a more stable thermal microclimate for the development of parasites, which together may predispose baboons to higher parasite diversity and prevalence. Furthermore exotic acacia species decrease the acidity of the soil and may thus increase the survival of eggs and larvae in the Peninsula. By contrast, pine trees, that are prolific in the Tokai region of the Peninsula, acidify the soils and thus similar to fynbos may have a negative impact on parasite life cycles.

Predation

High parasite intensity appears to render hosts more vulnerable to predation (Hudson *et al.* 1992). Watve and Sukumar (1995) showed that animals having less predatory pressure have greater parasite loads. Natural predators of baboon in the Cape Peninsula were eradicated over 100 years ago and humans and human-related activities (e.g., vehicles and power lines) are currently the main source of mortality (excluding infanticide) on the peninsula. The absence of natural predators that would presumably target specific age and sex categories of baboons may thus have a positive association with parasite diversity and prevalence in this population.

2.3.5 Parasite

Of the five parasite characteristics influencing mechanisms of infection, life cycle, transmission mode, location, host specificity, and pathogenicity, only two, namely life cycle and host specificity are investigated in this study.

Life cycle

Understanding the life cycles of the parasites discovered is important because the abiotic and biotic factors (as discussed above) will have a markedly different effect on parasites with a direct life cycle compared to those that require an intermediate host to be transmitted to the final host. Life cycles of the parasites found in this study can be seen in Appendix D.

Host specificity

Host specificity refers to the characteristic of a parasite that renders it capable of infecting one or more specific hosts at a particular stage of its life cycle (Nunn & Altizer 2006). Pathogens able to infect human, domestic, and wildlife hosts are very important from public health, conservation and economic perspectives (Cleaveland *et al.* 2001). According to a study effectuated by Woolhouse *et al.* (2001), the majority of pathogens can infect more than one species of host. Taylor *et al.* (2001) reported that 96% of the 287 helminth species found in humans are considered zoonotic. However, little is known about factors that influence the host range of parasites in natural populations.

In a review of studies on parasites of wild primates by Pedersen *et al.* (2005), up to 68% of primate parasites were reported to infect multiple host species (including species other than primates). For example, mountain gorillas and olive baboons seem to share parasite species (Hope *et al.* 2004). Interestingly, between viruses, protozoans, and helminths, helminths were associated with the greatest levels of host specificity. Approximately half of the helminths reported from primates were recorded as species-specific (Pedersen *et al.* 2005).

However, if we look at the studies that have been conducted on primate intestinal parasites, in particular on baboons, we find many suggestions of the zoonotic potential of the helminths. Meade (1984) suggested the sharing of *Trichuris trichiura* between baboons and humans and Ghandour *et al.* (1995) recorded the same species of parasites in baboons and humans in Saudi Arabia. In some cases, the role of the primate species as a maintenance host for a specific helminth has been proved under experimental conditions (Hira & Patel 1980; Zahed *et al.* 1996; Erko *et al.* 2001). In other studies, the conclusion of zoonotic potential of parasites reported is drawn from morphological studies of the parasite and from the available parasitological literature (Fenwick 1969; Munene *et al.* 1998; Mutani *et al.* 2003; Legesse & Erko 2004).

Reports on parasites of humans living in the communities of the Cape Peninsula that overlapped with troops were not available during the study period. The only study available reported on parasites of children in a suburb of the Cape Peninsula where baboons did not range (Adams *et al.* 2005). Prevalences for this study can be seen in Table 2.1.

If we want to confirm cross transmission between humans and nonhuman primates, the parasites must be identified to the species level and extremely detailed morphological analyses of adults are required (Chapman *et al.* 2006a). Laboratory experiments are also indispensable to prove cross transmission.

Due to the limited morphological characters of parasites, delimiting their species using microscopy can be difficult (Criscione *et al.* 2005). Molecular techniques are increasingly

Table 2.1 Prevalences of parasites found in children in a suburb of Cape Town (Adams *et al.* 2005).

Parasite	Prevalence in %
Trichuris	50.6
Trichostrongylus	0.1
Hookworm	0.1
Ascaris	24.8
Enterobius	0.6
Hymenolepis nana	2.2
Giardia	17.3

used as a main tool in the identification of species (McManus & Bowles 1996). Molecular methods are proving to be valuable in epidemiology and epizootiology (the study of disease transmission in humans and wildlife). PCR-based procedures enable the detection and characterisation of the genetic variability of infectious agents, particularly at the intraspecific level (Traub 2004). The sensitivity of PCR permits the amplification of genes or gene fragments from minute amounts of DNA; this is important because it is often difficult to obtain sufficient amounts of material from nematodes (Gasser 2001).

For example, molecular methods have been used to study genetic variation within *Oesophagostomum bifurcum* in humans and nonhuman primates in Ghana. This nematode, commonly called nodular worm, is thought to be a zoonosis. Different approaches, based on molecular and morphological analyses, revealed distinct groups in *O. bifurcum*, according to the species of primate host (Gasser *et al.* 1999; De Gruijter *et al.* 2004; De Gruijter *et al.* 2005b; Van Lieshout *et al.* 2005; De Gruijter *et al.* 2006; Gasser *et al.* 2006).

Molecular tools have also been used to prove cross-infection between humans and nonhuman primates. Singh *et al.* (2004) analyzed small subunit rDNA sequences obtained from human patients infected with malaria in Malaysian Borneo. The infections were previously identified via microscopy as *Plasmodium malariae*. Genetic research identified the parasite as *P. knowlesi*, which is morphologically very similar to *Plasmodium malariae* and is found in macaque monkeys. The confirmation of the parasite species has enabled researchers to focus on the important aspect of the potential transmission dynamics between humans and macaque monkeys (Singh *et al*. 2004).

Trichuris

Whipworms found in parasitological surveys in nonhuman primates are typically assumed to belong to the species *Trichuris trichiura*, the whipworm known to infect humans (Ooi *et al.* 1993; Cogswell 2007). The parasite is usually identified by the presence of the characteristic bipolar-plug egg in the faeces. Morphological studies on whipworm from nonhuman primates are rare. Ooi *et al.* (1993) compared the morphology of *Trichuris* sp. worms collected from macaques (*Macaca fuscata*) and baboons (*Papio papio*) to *T. trichiura* collected from humans, using light and scanning electron microscopy. The worms from the nonhuman primates were identified as *T. trichiura*; however, a slight variation was observed in a single morphological character namely, the length of spicule, suggesting that genetic analyses would be necessary to conclude that the worm was in fact the same species known to infect humans.

A thorough yet unsuccessful attempt was made to infect chacma baboons with *T. trichiura* eggs obtained from children in the Western Cape of South Africa (Fincham, personal communication). The eggs were incubated to an advanced embryonated stage and than dosed in large numbers to several baboons. Although a lack of successful infection is not proof that human *Trichuris* cannot infect baboons the results nevertheless question the assumption that *Trichuris* eggs found in the faeces of nonhuman primates in South Africa are in fact *T. trichiura* (i.e., the *Trichuris* of humans).

Various genetic analyses have been performed on the DNA of human *Trichuris trichiura*, including isolation and characterization of microsatellite loci (Barker & Bundy 2000), and random amplified polymorphic DNA analysis (Machado Martinez *et al.* 2003). However, the sequences of internal-transcribed spacer of ribosomal DNA (rDNA), of interest in this study, have as yet not been analyzed. The first and second internal-transcribed spacer (ITS-1 and ITS-2, respectively) provides genetic markers for the specific identification of a range of parasitic nematodes (De Gruijter *et al.* 2005b). Cutillas *et al.* (2002) have proved the existence of two separate *Trichuris* species in murid and arvicolid hosts, using polymerase chain reaction (PCR) techniques to amplify and sequence the ITS1-5.8S rDNA-ITS2 segment from the ribosomal DNA. No similar study has been performed on human and nonhuman primate *Trichuris*.

The aim of this study was to test the hypothesis that baboons living on the Cape Peninsula are cross-infected with *Trichuris trichiura* from humans. The ITS1-5.8S rDNA-ITS2 region was amplified by PCR from DNA extracted from Trichuris nematodes dissected from the guts of individual baboons from different Cape Peninsula troops. The amplified ITS1-5.8S rDNA-ITS2 regions were sequenced and compared to the ITS1-5.8S rDNA-ITS2 region of *Trichuris* sp. obtained from human patients.

2.4 Study host species

The chacma baboon, *Papio ursinus,* is found throughout southern Africa with the exception of the driest areas of the Kalahari and Namibia. Chacma baboons are able to live in many diverse areas; they are an omnivorous and opportunistic species, eating a large variety of food plants. The single most limiting factor in their distribution is the availability of water (Estes 1991). Chacma baboons primarily forage and travel on the ground but always use trees or rocks and cliffs as safe sleeping sites (Napier 1994). Chacma troops have home ranges that cover areas of 4-17km^2 and live in large, socially complex multi-male, multi-female semi-closed groups (Estes 1991). Mean group size for this species is 50 individuals (range, 20 to 100+) with approximately half of the troop members being sexually immature (< 6 years) (Fleagle 1988).

Adult male and female chacma baboons are organized into linear dominance hierarchies in which all females are subordinate to males. The majority of males emigrate from their natal troop between the ages of 6-7 years, while females are philopatric and form the stable core of the troop. Dominance ranks of females are relatively stable over time with daughters assuming ranks similar to their mothers (Melnick & Pearl 1986). Reproduction in chacma baboons is aseasonal but conceptions peak during periods of maximum rainfall when body condition is optimal. Oestrous cycles begin between 4.5 and 5 years of age in wild populations and first conception follows approximately a year later (Altman 1980; Smuts 1985). Sexual swelling is conspicuous during the follicular phase of a female's menstrual cycle and gestation lasts for approximately 187 days (Melnick & Pearl 1986; Napier 1994).

The Chacma baboons of the Cape Peninsula are the only protected population of this species, outside of closed National Parks, in South Africa. The population originally stretched from

Table Mountain to Cape Point and was contiguous with the neighbouring populations to the North and East of Cape Peninsula. As a result of the development on the peninsula and on the Cape Flats in particular, the population is today completely isolated (Kansky & Gaynor 2000). Despite being regarded as a unique ecotourism asset, both urban sprawl and previous management strategies have resulted in a marked decline (10% from 1997-2005) in the total population size. Despite the absence of natural predators, the mortality rate of baboons in peninsula troops is comparable to a wild troop under heavy predation pressure, with infant mortality accounting for 53% of all deaths (Van Doorn pers. comm.). Mortality is highest in troops that are in close contact with the urban fringe and individuals are killed by cars, attacked by dogs and electrocuted by above-ground power lines (Kansky & Gaynor 2000; Beamish pers. comm.). Currently there are approximately 376 individuals distributed amongst 13 troops in the Cape Peninsula. Of these troops, the largest troop (Tokai) with 120 members (currently splitting in three troops) is essentially isolated from the other 10 troops, which range in size from nine to 42 individuals. Given that this population is geographically isolated from other wild populations, it is possible that they will experience a genetic bottleneck. Reduced genetic diversity increases the susceptibility of organisms to a range of parasites and pathogens (Charlesworth & Charlesworth 1999) and may ultimately threaten the population with localised extinction.

The Cape peninsula baboons have effectively been forced into ever-closer contact with humans and this has resulted in a range of negative consequences for both parties. The baboons frequently sleep in and around urban areas and profit from the large volumes of human refuse discharged into their immediate environment. They have also become adept at raiding houses for food. In addition to living in close contact with the local population, baboons in the Cape of Good Hope (CoGH) section of the Table Mountain National Park (TMNP) have learnt to exploit poorly secured food-vending establishments (e.g., restaurants, takeaways, and picnic sites).

One solution to this human-wildlife conflict was the introduction of baboon monitors in 1998. Initially monitors were assigned to the two troops that had the most frequent contact with residents and they have subsequently been introduced to three more troops on the peninsula. These monitors function to minimize conflict by preventing the baboons from entering residential areas. Tentative results suggested that baboon monitors reduced the raiding frequency of baboons between five and 23 times (Kansky & Gaynor 2000).

Few studies have been conducted on the Cape Peninsula baboons. The first studies were conducted on baboon troops in the CoGH section of the TMNP, and consisted of observations on habitat, movement, diet, and population structure (Hall 1962; De Vore & Hall 1965; Millar 1970; Davidge 1976). Current studies are looking at the influence of human interaction on baboons from a socio-ecological perspective (Van Doorn pers. comm.). Parasitological investigations have never been conducted on the Cape Peninsula baboons.

2.5 Objectives and hypotheses

In order to establish how parasite infection dynamics are being affected by both natural and anthropogenic factors in the baboon population of the Cape Peninsula, this study has four major goals:

1. To determine the gastrointestinal parasite diversity and prevalence of the chacma baboon population of the Cape Peninsula, South Africa. To compare these data with those obtained for other baboon populations within South Africa and other baboon species, in various localities across the African continent.
2. To explore the influence of host-intrinsic individual factors (e.g., age, sex, reproductive status, and social status) on PSR, prevalence, and egg/larval output.
3. To investigate potential anthropogenic influences on parasite infection dynamics by comparing parasite data collected for six baboon troops subjected to varying levels of human interaction and anthropogenically transformed land.
4. To examine the potential for cross-transmission of helminths between baboons and humans by comparing the genetics of specific parasites with a high prevalence in both humans and baboons living within the Cape Peninsula (e.g., *Trichuris* spp.).

2.5.1 Hypotheses on host-intrinsic individual factors

Hypothesis on individual temporal variation:
Egg output shows temporal variation in the same host for different worm species.
Prediction:

There will be variation in egg output between samples collected within a few hours/weeks/months from the same individual.

Hypothesis on age and sex variations:

Parasite diversity and prevalence is influenced by the age and sex of baboons.

Predictions:

1. A positive association is expected between parasite infection and individual age.
2. Prevalence of the parasite *Strongyloides* will be higher in infants and juveniles than adults.
3. Males will have a higher diversity and prevalence of parasites than females, because of higher endogenous stress levels and higher levels of exposure to parasites.

Hypothesis on reproductive status:

Parasite prevalence and intensity of infection is influenced by host reproductive status.

Prediction:

Prevalence or egg output will be higher during the energetically costly stages of reproduction, including gestation and lactation.

Hypothesis on social status:

Parasite diversity and intensity are influenced by host social rank.

Prediction:

A positive correlation is expected between dominance rank and parasite infection risk and hence greater PSR and higher intensity are expected in higher-ranking individuals.

2.5.2 Hypotheses on host-intrinsic group attributes and habitat factors

Hypothesis:

Variation in helminth PSR, prevalence, and egg/larvae output between troops is influenced by both troop specific and ecological factors:

- Group size
- Host density
- Home-range size
- Home-range intensity of use, reuse of same areas (monitors)
- Range overlap between troops

- Overlap with humans and domestic animals
- Use of sleeping sites
- Diet (human food, human refuse)
- Rainfall (humidity)

Predictions:

The following, not mutually exclusive, predictions are derived from the above.

1. Group size: PSR and prevalence will be higher in larger troops.
2. Host density: PSR and prevalence will be higher in troops with a higher host density.
3. Home-range size: PSR will be higher in troops with larger home-range size; prevalence will be lower.
4. Home-range intensity of use and reuse of same areas: troops that use parts of their home range more intensively than other troops will show increased prevalence and intensity for the same parasite species, due to higher opportunities of reinfection.
5. Range overlap between troops: troops with a larger number of neighbouring troops and greater home-range overlap will show higher PSR and prevalence.
6. Overlap with humans and domestic animals: parasite PSR and prevalence will show a positive association with the percentage of overlap of troop's home range with land used by humans and domestic animals.
7. Presence of monitors: monitors herding baboon troops into the same areas on a repeated basis will increase the risk of infection and therefore helminth prevalence.
8. Use of sleeping sites: parasite prevalence and intensity will be higher in troops with fewer sleeping sites or a higher reuse rate of the same sleeping sites.
9. Diet: prevalence will be lower in troops with a higher proportion of human food in their diet, due to better nutritional status.
10. Rainfall (humidity): PSR and prevalence will be higher in troops where rainfall and therefore ground humidity are higher.

Table 2.2 shows a summary of the predictions mentioned above.

Table 2.2 Troop attributes and predicted correlation with various measures of infection risk.

Troop attributes	Affected measures of infection	Predicted correlation
Group size	PSR / Prevalence	Positive
Host density	PSR / Prevalence	Positive
Home-range size	PSR / Prevalence	Positive / Negative
Home-range intensity of use	Prevalence / Intensity	Positive
Range overlap between groups	PSR / Prevalence	Positive
Overlap humans and domestic animals	PSR / Prevalence	Positive
Presence of monitors	Prevalence	Positive
Number of sleeping sites	Prevalence / Intensity	Negative
Proportion of human food in diet	Prevalence	Negative
Rainfall (humidity)	PSR / Prevalence	Positive

CHAPTER THREE

MATERIALS AND METHODS

3.1 Study site

The study was carried out in three geographically distinct regions of the Western Cape Province of South Africa, namely the Cape Peninsula, the Overberg, and the Langeberg mountains (Figure 3.1.A). The Cape Peninsula was the principal study site and data were collected for six of the 13 baboon troops that comprise this population. A single troop (Pringle Bay troop) was sampled from the Overberg region, the nearest population (90 km to the East) to the geographically isolated Cape Peninsula population. A single troop was sampled from the Wildcliff Nature Reserve, 296 km from Cape Town, in the Langeberg mountain range. A brief description of each study site follows.

3.1.1 The Cape Peninsula

The Cape Peninsula (470 km^2) is located at the south-western tip of the African continent and stretches from the city of Cape Town to the Cape of Good Hope (CoGH) section of the Table Mountain National Park (TMNP) (latitude 33°55' - 34°21' S; longitude 18°25' - 18°28' E). It is characterized physiographically by high topographical heterogeneity, extreme variation in annual rainfall, and nutrient-poor soils (Cowling *et al.* 1996). The Peninsula is a globally important hot spot of biodiversity for higher plants and invertebrates. The Table Mountain National Park (221 km^2) is an integral part of the Cape Floristic Kingdom, the smallest but richest of the world's six floral kingdoms (Cowling *et al.* 1996). The predominant vegetation is fynbos, a species-rich but nutrient poor, fire-prone, sclerophyllus shrubland (Cowling *et al.* 1996). The vertebrate fauna is characterized by moderate species diversity, low endemism, and low numbers. Chacma baboons are the only nonhuman primate species found on the peninsula.

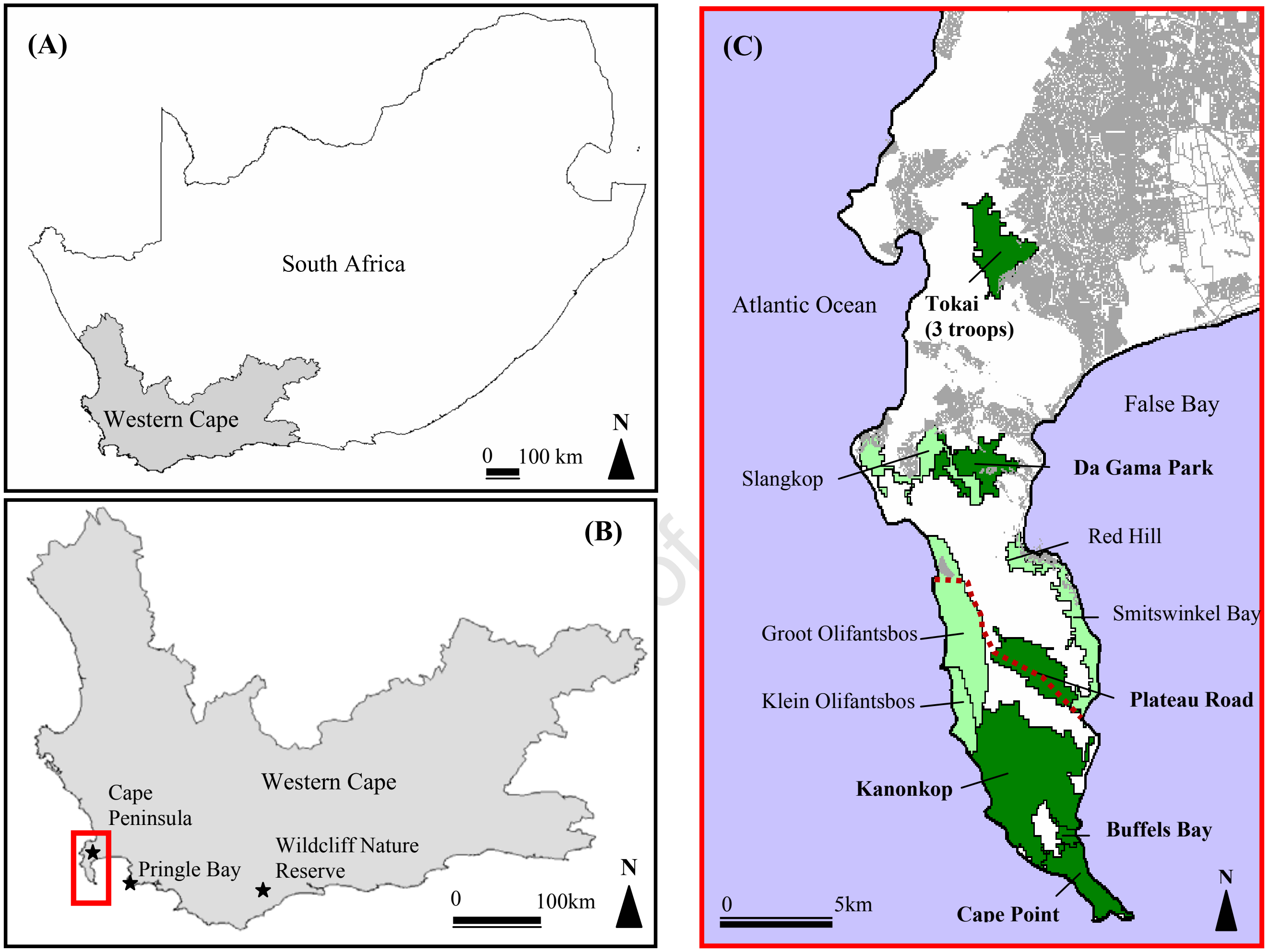


Figure 3.1 A: Location of the Western Cape Province in South Africa. **B:** Location of the three collection sites in the Western Cape Province. **C:** The home ranges of the study troops (dark green) and other troops (light green) in the Cape Peninsula. Urban areas are shaded in grey and the border of Cape of Good Hope section of the Table Mountain National Park is outlined in red (dashed line).

The Cape Peninsula has a Mediterranean-type climate with well-defined seasons (Davidge 1978). Cumulative rainfall, minimum and maximum temperatures, and the daily temperature were recorded daily at 08h00 in three locations within the Cape Peninsula (data supplied by the South African Weather Service). The first weather station was located in Cape Point (station 00048919, -34.35°S, 18.49°E, 228 m elevation), the second in Slangkop (station 00045492, -34.15°S, 18.32°E, 8 m elevation) and the third station was located at the Cape Town International Airport (station 0021178A3, -33.97°S, 18.60°E, 42 m elevation). Temperatures of these weather stations were pooled to create an average for the whole Cape Peninsula. In the case of Tokai, it had been demonstrated already that data recorded in the plantation and data recorded at the Cape Town International Airport station were very similar (Hoffman 2006). Rainfall data for the three weather stations were also pooled in order to obtain an average for the Cape Peninsula. However, since patterns of rainfall differed markedly for Tokai, which is in the lee side of a large mountain (Constantiaberg), data specific to the troop in this region were obtained from the South African National Parks (SANParks) weather station situated within the Tokai plantation.

In winter (May to August), cold fronts swept in from the Atlantic Ocean bringing strong north-westerly winds with a mean speed of 30 km/h at Cape Point (Cowling *et al.* 1996) and heavy rainfalls. Rainfall in winter (2006 and 2007) ranged from 503 to 687 mm. The winter months were thus cool and wet, with an average daily minimum temperature of 10.5°C during the study period. Summer (November to February) was warm (average daily maximum temperature of 23.5°C) and dry with strong winds (mean of 40 km/h) from the Southeast at Cape Point (Cowling *et al.* 1996). It is thus obvious that there is marked seasonal variation within the Peninsula and furthermore that this Mediterranean-type climate differs dramatically from that typically experienced by savannah baboons at lower latitudes.

Human density within the Peninsula was limited, until relatively recently, by the low carrying capacity of the fynbos biome. The arrival of Europeans in 1652 brought major changes, including the conversion of the lowland areas to agricultural land use practices. After the colonization of the Cape, both direct and indirect impacts on the natural ecosystems of the Peninsula escalated dramatically, and by 1994, some 65% of original natural habitat was either transformed by urbanization and agriculture, or invaded by introduced exotic plants (Cowling *et al.* 1996).

The current human population of Cape Town is approximately 3.1 million, mostly the result of recent immigration of people from other parts of South Africa and the African continent. The rapid development and expansion of informal settlements over the last decade (a combination of immigration and poverty) is having a marked adverse impact on the remaining lowland vegetation within the major metropolitan areas of Cape Town. Informal settlements adjacent to the Table Mountain National Park have greatly increased the risk of wild fires that originate from uncontrolled cooking fires. Another cause of ecological pressure comes from the rapid development of tourism. More than a half of international tourists visiting South Africa visit the CoGH section of the TMNP (830,000 in 1999) with domestic visitor numbers even higher at 3.8 million in 1999.

3.1.2 Pringle Bay

The Pringle Bay troop usually ranges between the coastal villages of Pringle Bay (latitude 34°21'S, longitude 18°49'E) and Rooiels (latitude 34°18' S, longitude 18°49' E), which are approximately 3 km apart along the same stretch of coastline. The exact home range of the troop has not yet been established. The two villages fall within the Kogelberg Biosphere Reserve and are separated by a small mountain called "Klein Hangklip". The vegetation type in this region is mainly composed by indigenous fynbos. The climate is very similar to that described for the Cape Peninsula. Mean annual rainfall for 2007 was 632 mm, and averages of daily temperature minima and maxima were, respectively, 13.8 and 21.6°C.

3.1.3 Wildcliff Nature Reserve

Wildcliff Nature Reserve is located approximately 20 km north of Heidelberg, in the Langeberg Mountains and comprises an area of 955 ha (latitude 33°58.5' - 33°55.9' S; longitude 20°58.9' - 21°3.0' E), with elevations from 290 m to 1130 m (Giddy 2007; Pebsworth 2008). The area is comprised of deep valleys with afromontane forest, rocky mountaintops and high meadows of fynbos. The lower parts of the reserve have been used for cattle farming (and other agricultural practices) over the previous 150 years and include extensive tracts of exotic vegetation including cluster pine stands and the highly invasive black wattle. The property was purchased in 2007 and proclaimed as a nature conservancy with a view to restoration and long-term conservation of the flora and fauna. The annual rainfall for 2007 was 654 mm, and the average daily temperature minima and maxima were 11.5 and 24.8°C, respectively.

3.2 Study troops

The selection of six troops out of a total of 13 currently living on the Peninsula represented a compromise between limited human resources (i.e., people for data collection) and the desire to maximise the variation in both ecological and anthropogenic variables for each troop. The diverse range of both anthropogenic and ecological variables that the Peninsula troops experience suggested that understanding host-parasite transmission mechanisms would be best achieved by a comparison across multiple troops rather than a more detailed investigation on one or two troops.

The location of the six study groups of chacma baboons (*Papio ursinus*) and their relative home ranges are shown in Figure 3.1.B. Three of the six Peninsula study troops, Cape Point, Buffels Bay, and Kanonkop, ranged within the CoGH section of the TMNP (77.5 km^2) whilst the remaining three ranged outside of this area in land that is adjacent to both urban and agricultural land use practices. All troops are within 30 km of one another (in a straight-line direction) but only limited movement of animals between the troops outside the park is possible due to partial isolation from urban sprawl.

Censuses had been conducted on the Peninsula troops since 1998 by various researchers. Troop composition of the six Cape Peninsula study troops during the study period is provided in Table 3.1 (Beamish unpubl. data). Mean group size was calculated as the mean number of individuals per group over the study period. The troops sampled were homogeneous with regard to sex ratio, age structure, and social structure. A detailed description of each troop follows in the next section.

Table 3.1 The composition (age and sex categories) of the six study troops, including initial and mean group size over the study period. M=male, F=female.

Group	Adults		Subadults		Juveniles		Initial group size	Mean group size
	M	F	M	F	M	F	M & F	M & F
Cape Point	2	12	0	3	5	6	28	25
Buffels Bay	2	5	0	1	1	3	12	11
Kanonkop	6	12	0	1	12	10	41	42
Plateau Road	1	14	0	3	9	9	36	40
Da Gama Park	4	13	1	2	8	8	36	37
Tokai	7	34	5	2	39	28	115	122

Age classification refers to the age when the individual was first observed; data from Beamish (unpubl.), sources of age classification: Altman 1980.

3.2.1 Cape Point

This troop's home range included the southern most section of the CoGH section of the TMNP and extended northwards to Platboom on the West Coast and Buffels Bay on the Eastern coast of the peninsula. The troop members were adept at raiding tourists for food and thus had a high rate of human contact, despite being within a national park. Monitors were employed to chase the troop away from areas that tourists frequent (i.e., the restaurant and car park) with only limited overall success. The vegetation within the home range was comprised almost exclusively of indigenous fynbos with some exotic grasses and annuals in low-lying areas.

3.2.2 Buffels Bay

This troop was the northern neighbour of the Cape Point troop and frequented the low-lying land within the Buffels Bay region of the CoGH. The troop comprised 11 individuals with one adult male and five adult females. The troop spent the majority of their time in the vicinity of Buffels bay where they regularly raided both people and rubbish bins at the public open picnic sites. The majority of their home range was comprised of fynbos interspersed with open sand dunes and exotic grasses at picnic sites adjacent to the intertidal zone. The home-range habitat also included cliffs, riverine vegetation, a few cleared patches of exotic vegetation, trees, human constructions (i.e., the visitor centre), and a road. All adult troop members were identifiable by distinctive corporal marks and had been named individually.

3.2.3 Kanonkop

This troop was regarded as the least impacted by anthropogenic influences on the Cape Peninsula and within the CoGH section of the TMNP. Kanonkop home range was on the northern border of the Cape Point home range and both northerly and west of the Buffels Bay troop. The troop members were not habituated to close human presence and had to be followed at a distance of at least 10 meters when collecting samples. The troop numbered 42 individuals, including five adult males and 15 adult females and foraged predominantly on fynbos vegetation with some exotic grasses and annuals being available in low-lying areas.

3.2.4 Plateau Road

The troop's home range included a longitudinal tract of land adjacent to the Plateau Road that runs along the eastern border of the CoGH section of the TMNP. The home range included a high density of exotic vegetation including plantations of pine and eucalyptus and dense almost impenetrable stands of exotic acacia spp. Exotic vegetation was spatially coincident with low-lying land and a small number of houses on small holdings including an ostrich farm. High lying areas were comprised predominantly of fynbos. The troop was comprised of 40 individuals, with only one adult male and 14 adult females. A second adult male was killed by domestic dogs in February 2006. The troop had been habituated to the close observation since February 2004. All adults had been identified by distinctive corporal marks and named individually. Detailed behavioural observations on this troop were performed during a parallel study (van Doorn, in prep.) which together with this study allowed for the dominance rank of all adult females to be determined. The troop frequently travelled along the Plateau road that runs the length of their home range and accepted food offerings from tourists in vehicles that stopped to view the baboons (Kansky & Gaynor 1998). Furthermore, the baboons regularly visited the ostrich farm, established in 2000, to raid ostrich feed.

Interactions with humans also took place with informal traders close to the entrance gate of the CoGH section of the TMNP. These traders made frequent use of the bushes in the area as an open latrine and thus the troop were exposed directly to human faeces when traversing this section of their home range.

3.2.5 Da Gama Park

The Da Gama Park troop was comprised of 37 baboons, 17 of which were individually identifiable adults including four males and 13 females. Detailed behavioural observations on this troop were performed during a parallel study (van Doorn, in prep.) which together with this study allowed for the dominance rank of all adult females to be determined. Historically all the males within this troop were killed and subsequently new males were reintroduced while others subsequently immigrated from the neighbouring troop - Slangkop. Slangkop itself was originally a fission troop from Da Gama Park and thus all the adult females and many of the adult males in these two troops are presumed to be close relatives. The troop's home range included riverine patches of pine trees, dense acacia thickets, patches of cleared exotic vegetation and natural fynbos interspersed with low densities of exotic vegetation. A large residential area with a general store sports fields and horse stables were found at low altitudes within the home range. The troop was herded by baboon monitors on a daily basis to exclude them from the urban edge and thus to reduce human-baboon conflict. Despite the best efforts of the monitors, raiding was a regular occurrence and both human and domestic animal encounters were frequent. Furthermore, the baboons came into contact with both human and domestic animal faeces (e.g., dogs, cats, and horses) and in turn, the residents were frequently exposed to the faeces of the baboons.

3.2.6 Tokai

The sixth study troop, Tokai, was the most northerly of all the peninsula troops and the most isolated of all the peninsula troops. It was comprised of ca. 122 individuals with nine adult males and 35 adult females. Sub-trooping was a relatively frequent event with the most permanent sub troop (named John Travolta by the local residents) comprising 12 individuals (one adult male and four adult females). A further split in the main troop was evident in the winter of 2006. All sub-troops lived predominantly within the exotic pine and eucalyptus cultivated part of the Tokai plantation but all of them engaged in raiding behaviour in the adjacent vineyards and urban areas. Baboon monitors have worked erratically on this troop since 2001 with only limited success in preventing the troops from raiding agricultural land.

3.2.7 Pringle Bay

This troop was comprised of ca. 26 individuals including two adult males and eight adult females. The troop was observed to frequent the village of Pringle Bay with the occasional visit to the neighbouring town of Rooiels. The area was characterised by fynbos vegetation with patches of exotic vegetation including eucalyptus, pine, and acacia spp. Low-lying regions, including the towns, provided abundant access to exotic grasses, annuals, and fruit trees. The troop also had frequent access to human refuse and faeces from domestic animals (e.g., cats, and dogs).

3.2.8 Wildcliff

Two troops of baboons ranged in Wildcliff Nature Reserve including a small troop of 12-13 individuals and a large troop of approximately 50 individuals (Fust 2008). The number of adult males and females in each troop was not known at the time of the study. Samples for this study were collected from the large troop, which was not habituated to close human observation. The troop slept within a gorge and typically foraged in dense stands of exotic pine and black wattle including a large meadow previously used for grazing cattle and comprised almost exclusively of exotic grasses and annuals.

3.3 Study period

Data collection in the Cape Peninsula was carried out from July 2006 to August 2007. All baboon faecal samples used for analysis were collected during this period, which included two winter seasons and the summer season in between. Faecal samples from Pringle Bay were collected between February and May 2008, while Wildcliff data were collected in October and November 2007.

GPS data for the Plateau Road and Da Gama Park troops were collected in 2004 and 2005 as part of another study (van Doorn unpubl. data). Home ranges vary minimally on an annual basis (van Doorn, pers. comm.) and thus the home-range estimate for 2005 was considered to be a reliable estimate as a troop attribute for the samples collected in this study during 2006 and 2007. GPS and behavioural data for the rest of the Peninsula troops (Cape Point, Buffels Bay, Kanonkop, and Tokai troops) were collected between 2006 and 2008 as part of other studies (Hoffman unpubl. data; Lewis unpubl. data; Stephenson unpubl. data).

3.4 Parasitological analyses

3.4.1 Collection and preservation of baboon faecal samples

Sample size

A total of 616 faecal samples were collected in a non-invasive way from eight baboon troops between 2006 and 2008. Every attempt was made to sample each individual only once during a field day; however, as individual identification was not possible in all the troops, it is possible that some individuals were sampled more than once in a day. Only in one case, the analysis of daily intra-individual variation in parasite infections, I used samples collected on the same day from the same individual to assess the variability across samples in estimating the parasite specie richness (PSR) of helminths and protozoa. The time elapsed between the collection of the first and second sample varied between 10 minutes and two hours, and all samples were collected within the first three hours on each day.

Repeat samples for one individual were present, since the same troops were visited several times during each season. Faecal samples were collected immediately after defecation to avoid contamination; it was not however always possible to match the specific host with the faecal samples. Table 3.2 shows the number of samples collected from unknown versus known individuals. Different categories of samples were used for the various different analyses, in accordance with the question(s) being investigated. Thus for example analyses that required individual-level identification such as the effects of social status on parasite species richness (PSR) and prevalence were investigated using individuals from the Buffels Bay, Da Gama Park, and Plateau Road troops in which all individuals were identified. For the analysis of intra-individual temporal variation, I used a minimum of four samples collected from the same individual on different days. The interval of time between repeat samples varied from one to 221 days. For each parasite taxon, I calculated the percentage of all samples for each individual that were positive.

While every attempt was made to sample as consistently as possible between seasons and across troops, this proved to be a very difficult task with the terrain for certain troops making it exceptionally difficult to access sleeping sites (e.g., Cape Point) where samples were most readily obtained. The variation in sample size and level of detail for each sample influenced the sample size used in all subsequent statistical analyses, the details of which are provided below.

Collection time

Baboons did not seem to have a preferred time for defecation. Samples were collected at any time between 07:00 and 18:30. In an attempt to clarify whether presence of infectious stages in faeces varied between samples collected at different times, a test was done comparing all hours between 08:00 and 17:00, using only one troop and one season in order to control for these potentially confounding factors. The Tokai troop was chosen for this analysis as samples were most evenly spread across all time periods; only summer samples were included in the analysis (n=50). Parasite species richness, prevalence, and egg output did not differ between the different time categories throughout the day (see Appendix B for results of statistical tests).

Collectors

Faecal samples were mainly collected by the principal investigator, but also on occasion by volunteers. Precise guidelines and training made sure that samples were collected in the same manner by all observers. Tokai troop summer data were chosen again to compare parasite infection indices between samples collected by the main researcher (n=36) and samples

Table 3.2 Total sample size of faeces from each study troop and level of detail (individual identity, sex, and age) for each sample collected across all troops.

Troop	Known individual	Known age and sex	All unknown	Total number of samples
Buffels Bay	48	3	11	62
Cape Point	0	7	14	21
Kanonkop	0	0	68	68
Plateau Road	101	46	47	194
Da Gama Park	63	34	17	114
Tokai	3	66	3	72
Pringle Bay	3	12	20	35
Wildcliff	0	0	50	50
Total				**616**

collected by other observers (*n*=14). Parasite taxa diversity and prevalence did not show any significant difference between collectors (see Appendix B for results of statistical tests).

Collection procedure

The permit for collection of faecal samples inside the CoGH section of the TMNP and the Tokai plantation was obtained from South African National Parks, section Table Mountain National Park. All samples were collected within 15 minutes of defecation and initially examined macroscopically for adult nematodes and tapeworm proglottids. The part of scat not touching the ground was collected with a plastic bag and homogenized well. Two replicate samples, approximately 1 g in weight, were then taken from each scat and placed within two hours in numbered plastic vials of known weight containing 3 ml 10% formalin, where they were homogenized well again. This procedure allowed the subsequent calculation of the sample weight. Each sample was labelled with date and time of defecation, troop and identity of the animal that produced the sample (where possible) and included a description of the scats' consistency.

Faecal samples were stored at ambient temperature in 10% formalin, for three months on average, before being processed (84% of the samples stored for less than six months; 16% of the samples stored between six and 10 months). The vials containing faeces were weighed again in order to calculate the final sample weight. We aimed to collect samples of 1.00 g weight. Most of the samples (68.2%) weighed between 0.50 and 1.50 g; 12.6% weighed between 1.50 and 3.48 g. 19.2% of the samples weighed less than 0.50 g. The variation was largely attributed to spillage of formalin during the collection procedure and was considered when selecting samples for the calculation of egg output.

3.4.2 Faecal sample processing

A modified formalin-ether sedimentation technique (Allen & Ridley 1970) was performed for all faecal samples. All samples were processed in the same laboratory, on the premises of the Medical Research Council of Tygerberg, South Africa. Faecal samples in formalin were homogenized thoroughly. To remove debris, the faecal solution was strained through a polyamide kitchen sieve (mesh size of about 500 µm) into a 15 ml centrifuge tube. More formalin was added to adjust the volume to 7 ml. The fat in the resulting fluid was removed by emulsifying the sample with 3 ml of ether added to the tube followed by vigorous shaking for 2 minutes and centrifugation at 2,000 rpm for 3 minutes. The resulting top layers of fat and supernatant were discarded, leaving behind only a pellet at the bottom of the tube containing the parasite eggs and cysts. A couple of drops of 10% formalin were added to the pellet to avoid desiccation and preserve the contents until microscopic examination.

3.4.3 Microscopic examination

The sediment was thoroughly mixed and a droplet of Lugol's iodine was added in order to facilitate the identification of protozoan cysts. The solution was placed on a slide, covered with a cover slip, and systematically scanned with a microscope at a magnification of 100, 200, 400, and 600 times. Time spent analyzing a sample varied between 30 and 60 minutes. The majority of samples collected from the Cape Peninsula troops were analyzed by an expert parasitologist of the Medical Research Council in Tygerberg. A small subset (*n*=51) of faecal samples was analyzed by two expert parasitologists at the University of KwaZulu-Natal in Durban. This subset was only used for analyses on variation of PSR and parasite prevalence among female baboons of different social status and only after ensuring that the variations of parasite infection measures calculated by the three analyzers were not statistically significant. A separate group of the samples collected in the Cape Peninsula (*n*=117) was used by the main researcher to learn how to identify helminth and protozoan infectious stages. These samples were not included in further analyses. All the samples collected from Pringle Bay and Wildcliff troops were microscopically analyzed by the main researcher after having acquired the ability to reliably identify the different parasites.

Parasite identification

Helminth eggs and larvae, and protozoan cysts were identified using their morphology, shape, size, and other visible structures. Representative specimens of eggs and larvae were photographed (Olympus Camera). Measurements of eggs (length and width) were made to the nearest 0.5 µm at a magnification of 200 times using an ocular micrometer fitted to a compound microscope. About 10 stages of the same morpho-type eggs (not damaged or deformed) were measured per sample, whenever measurements were done. Minimum and maximum size, mean and median size, and interquartile range (IQR) was calculated for each morpho-type. The eggs dimensions were also compared with the block graphs constructed by Goldsmid and Rogers (1978) for four common strongyles of baboons from southern Africa (*Strongyloides fuelleborni*, *Oesophagostomum* sp., *Ternidens deminutus*, and *Trichostrongylus* sp.).

Due to the low reliability of identification of parasite eggs, larvae, and cysts by microscopic analysis (Gillespie 2006), the parasites were identified to the level of family or genus. Helminth identification was done in collaboration with Colleen Archer, Pollution Research Group, University of KwaZulu-Natal, and Vera Adams, NIRU, MRC, and followed Brack (1987).

Parasite species richness

Margolis *et al.* (1982) defined PSR as the number of different parasite species per host individual, social group, or other. All samples collected (Table 3.2) were included for PSR calculations. Another useful index of infection is represented by the frequency of multiple-species infections (i.e., the proportion of the population with individuals hosting >1 species of parasite; Chapman *et al.* 2006b). In this study, the proportion of samples with >1 parasite species was used for analysis.

Parasite prevalence

Prevalence is defined as the number of individuals of a host species infected with a particular parasitic species divided by the number of hosts examined (Stuart & Strier 1995) and is usually expressed as percentage or proportion (Margolis *et al.* 1982; Bush *et al.* 1997). Due to the relatively large number of troops analyzed in this study, only adult individuals of three of the six study troops were individually identified and recognizable. Consequently, most of the samples collected (65%) could not be attached to known individuals and this caused two potential problems: the repeated collection of samples from the same individuals and the inability to calculate prevalence based on the number of individuals infected. It has been demonstrated that the use of the number of samples instead of the number of individuals to calculate the prevalence can create a reporting bias (Huffman *et al.* 1997; Mühlenbein 2005). I attempted to minimise the impact of this problem by collecting samples from troops comprised of unknown individuals over brief periods (e.g., two hours after sunrise) on a particular day. Using this approach, I was able to collect samples from up to 70% of the individuals within a troop on a given morning, which greatly reduced the probability of pseudo replication on a given day. However, repeat samples were likely on repeat days, which while also kept to a minimum were necessary to obtain an adequate minimum sample size. Thus, the prevalences estimates reported in this study should be viewed as indices of prevalence (*sensu* Chapman *et al.* 2006b). In an attempt to verify the existence of a difference between prevalences calculated from number of animals infected and number of faecal samples infected, some tests were performed on samples collected from the three troops with known individuals: Buffels Bay, Da Gama Park, and Plateau Road.

As a first step, the number of repeat samples to be analyzed per each individual had to be chosen. This was because the number of cumulative samples analyzed per individual appears to play an important role in the number of parasite species found in an individual host, and consequently on the prevalence calculated for a group of hosts. Meade (1984) found a significant positive correlation between number of faecal samples examined per individual and number of helminth species reported for that individual. However, the correlation ceased to be significant when more than ten samples were examined for the same individual. She speculated that thereafter, there was likely to be little change in number of species reported for an individual whether 10 samples or even 20 additional samples were collected from that individual. I thus correlated the cumulative number of parasite species identified with the number of samples analyzed for known individuals. This allowed for a calculation of the minimum number of repeat faecal samples from one individual that was necessary in order to eliminate the variance caused by sample size alone. As a second step, prevalences calculated on the basis of number of individuals infected were compared to prevalences calculated on the basis of number of samples infected.

Output of helminth eggs and protozoan cysts

Generally, egg output is no longer considered as a precise measure of parasite infection (Gillespie 2006) and might be used as an index of infection only if results are in concordance with other indices (Chapman *et al.* 2006b). The calculation of eggs per gram of faeces can be biased by the inexact weight of the sample due to potential evaporation of the storage liquid between field trips and laboratory analyses. Here, only samples with a weight > 0.20 g were utilized for egg counts in order to obviate this potential problem.

The total number of eggs of each species of helminth was counted by scanning slides using the 10 times objective lens of a compound microscope. Egg counts estimated per gram of faeces may be influenced by the consistency of the scats from which sample was taken with loose scats having a lower egg count as a result of dilution. In an attempt to control for this source of variation I used a multiplication factor for the five categories of consistency assigned to each scat upon sampling (*sensu* Archer *et al.* 1997). Scat consistency factors are provided in Table 3.3.

Egg counts were expressed quantitatively per 1 g of faeces according to the following formula: Number of eggs/g = (Egg count)*(consistency factor)/(weight of sample in g)

Cyst output values were divided into five different classes while being observed under the microscope. These classes are shown in Table 3.4 and were used for all subsequent analyses on protozoan cyst output.

3.4.4 Coprocultures

The similarities in size and appearance of the eggs of different species of gastrointestinal nematodes are such that their differentiation is extremely difficult. Third-stage larvae of these nematodes are however sufficiently different and may be used to distinguish between

Table 3.3 Scat consistency factors used to adjust egg counts.

Scat consistency	Multiplication Factor
Formed (F)	Egg count x 1.0
Semi-formed (SF)	Egg count x 1.5
Mushy (M)	Egg count x 2.0
Mushy-diarrhoea (MD)	Egg count x 3.0
Diarrhoea (D)	Egg count x 4.0
Watery (W)	Egg count x 4.5

Table 3.4 Classes of protozoan intensity of infection.

Class	Cysts per high power field (e.g., 20 x)	Cysts per coverslip
0	Not present	Not present
1	1-2	$1 < n < 800$
2	2-50	$800 < n < 20,000$
3	50-200	$20,000 < n < 80,000$
4	> 200	> 80,000

different genera, and even species in some cases. Strongyle eggs and rhabditiform larvae from 10 scat samples taken from Cape Peninsula baboons were allowed to develop to the filariform stage (L3) by means of coproculture (Harada & Mori 1955). Larvae and adult helminths were photographed using an Olympus Camera and the pictures were sent to DPDx (Division of Parasitic Diseases, Centers for Disease Control and Prevention, Atlanta, USA) for identification.

3.4.5 Opportunistic necropsies

Opportunistic necropsies were performed whenever dead baboons were brought to the University by members of the public or welfare agencies. Necropsies allowed for the isolation of adult and immature gastrointestinal parasites. Three baboons from Da Gama Park, one from Cape Point and one from Tokai were examined during the study period. The entire gastrointestinal tract of each baboon was dissected out (stomach, small intestine, large intestine, and colon) and then removed from the body cavity of the individual. Each section of the tract was then washed separately as described in Gillespie (2006). Recovered adult helminths were preserved in 70% ethanol and subsequently identified using Brack (1987) to match the parasite eggs found in faeces to the adult worms in the gut to enable a positive identification.

3.5 Troop attributes and habitat factors

3.5.1 Social rank

Dominance ranks were calculated for the adult females of two troops, Plateau Road and Da Gama Park, on the basis of detailed behavioural observations recorded in 2004 and 2005. Briefly, the number of occurrences in which one individual displaced another, or won an aggressive encounter over a resource with another troop member, was recorded for every possible pair of adult individuals in the troop. To derive a dominance hierarchy from observations of the interactions between individuals, the frequency of performance of all dominant behaviours were arranged in a matrix (*sensu* Martin & Bateson 1993). All individuals were then arranged, highest to lowest, into a dominance hierarchy and their relative rank (low, medium, and high) assigned accordingly.

3.5.2 Troop size and host density

Mean troop size was calculated as the mean number of individuals per troop over the study period (Table 3.1). Host density was calculated by dividing the total area of the home range (see below) by the mean troop size.

3.5.3 Home-range size

Quantitative data on home-range size were collected during the course of other parallel research projects on the Peninsula troops. GPS data points were collected using hand held

GPS devices and these data were then exported into Excel; GPS latitude and longitude positions were captured in degrees, minutes and seconds and then transformed into decimal degrees. The GPS points were then imported into Arcview 3.3 (Universal Tranverse Mercator projection, Spheroid WGS 84 datum, with Central Meridian 19, Reference latitude 0, and Scale factor 1). Points were overlaid onto a year 2002 geo-referenced satellite image for the Peninsula region, provided by South African National Parks.

The areas used by each troop were broken down to a grid of quadrats, each composed of 150 square meters using the geographic information system software package, ArcGIS 3.3. Home-range size was computed by superimposing 150 x 150m quadrats over the data points. Home-range size was calculated by adding all entered quadrats to quadrats that were enclosed by at least 3 sides. Isolated cells were connected to the closest quadrats using the most direct route The total home-range size was calculated by multiplying the number of cells entered by the standard cell area, and an annual point frequency value was calculated for each entered cell by counting the number of GPS data points within it (Hoffman, pers. comm.).

3.5.4 Intensity of home-range use

The frequency of home-range use was determined by counting the number of times a troop entered each quadrat within the home range. This number was then divided by the total quadrat frequency to yield a percentage of total use (i.e., intensity) which allowed for a meaningful comparison between troops and seasons based on different sample sizes (van Doorn unpubl.; Hoffman unpubl.).

3.5.5 Home-range overlap between troops

This variable was estimated as the percentage of the total area comprising each troop's home range that overlapped with that of a neighbouring troop. For troops which had neighbours lacking detailed spatial information namely, Kanonkop, Plateau Road, and Da Gama Park, the percentage overlap was determined from home ranges that were estimated from known sightings of the troops over a nine-year period (1998-2007) by various researchers who have worked on these particular troops (Kansky & Gaynor 1998; van Doorn unpubl. data; Beamish unpubl. data).

3.5.6 Home-range overlap with urban land and with transformed land

Overlap with urban land was calculated as the percentage of the troop's home range that overlapped with land used specifically for human activities including residential areas, areas of recreation (picnic areas, restaurants, markets, visitor centres). Overlap with transformed land was calculated in the same way but included agricultural land and exotic vegetation.

3.5.7 Number of sleeping sites

Sleeping sites were determined by following the troops on foot and recording the exact location where the troop slept using a hand held GPS. The extent of a given sleeping site was fixed at 50 m in all directions from the centre point of the sleeping site. Any GPS point outside of this circle at which the troop slept on a different occasion was considered to be a separate sleeping site.

3.5.8 Proportion of anthropogenic food sources in diet

It was not possible to quantify the amount of human derived food that the members of each troop consumed over the study period. However, long term studies on all six troops (van Doorn unpubl. data; Hoffman unpubl. data; Lewis unpubl. data) do allow for the use of an index of human food consumed: 1=low, 2=medium, 3=high, where low refers to a very infrequent (less than once a month) and mostly opportunistic encounter with human derived food (e.g., food discarded from a vehicle), medium refers to a fairly predictable encounter with human food but at a low frequency (e.g., weekly garbage collection) and high refers to an almost daily inclusion of human food in the diet (e.g., actively raiding gardens, farms, and houses).

3.5.9 Rainfall

Data on precipitation was obtained from the South African Weather Service, which has several weather stations located in different regions of the Cape Peninsula. Data on precipitation in the Tokai plantation were obtained from the South African National Parks

(SANParks) weather station within the Tokai plantation. Further details can be found in the section on Cape Peninsula climate.

3.6 Molecular analyses

3.6.1 Collection of specimens for molecular analysis

Adult specimens of the nematode *Trichuris* sp. were collected from the gastrointestinal tracts of five dead baboons that had been preserved through freezing. Several *Trichuris* worms were collected from the large intestines of three adult females of the Da Gama Park troop (DGI, DGII, and DGIII), one adult male from the Cape Point troop (CP), and one infant female from the Groot Olifantsbos troop (GOB). All worms were stored in 99% ethanol until required for DNA extraction.

Two adult human whipworms (*T. trichiura*) were obtained in 2000 from human patients from the city of Kumba, Cameroon, following the administration of a dose of anthelmintic drug (pyrantel). Both worms were then frozen at -80° C before DNA extraction. The latter two samples were processed and analyzed at the School of Biology at the University of Nottingham (UK) and thus the following methodology is specific to the *Trichuris* sp. obtained from the baboons in the Cape Peninsula.

3.6.2 Molecular methods

Extraction of DNA from adult worms

Worms were washed extensively in 0.9% saline solution. Genomic DNA was then extracted from whole individual worms using a QIAamp Tissue Kit (Quiagen) following the manufacturer's protocol, but with the following modifications (*sensu* Traub *et al.* 2002). An adult worm from each individual baboon was suspended in 180 µl of ATL tissue and 20 µl Proteinase K (10 µl/ml) and incubated within a 1.5 ml Eppendorf tube overnight at 56°C. For complete breakage of the tissue and cells, two steel beads were added to the solution and the tubes were subjected to strong shaking for four minutes in a Gyromixer (Fast and Fluid Management, Sassenheim, the Netherlands) 200 µl of buffer AL was then added to the tube which was vortexed for 10 seconds and incubated at 70°C for 10 minutes. The suspension was then centrifuged at 14,000 rpm for one minute, the lysate transferred to a QIAamp MinElute Column, and vortexed again at 8,000 rpm for one minute until the column was empty. Pellets were washed in two steps with 500 µl AW buffer containing ethanol, vacuum dried for three minutes to remove any remaining ethanol and resuspended in 30 µl elution buffer, to rinse the DNA off the spin column filter, for five to ten minutes. Genomic DNA was quantified by a spectrophotometer reading at A_{260}nm on a NanoDrop, and was analyzed by electrophoresis through a 1.5% tris-borate-EDTA (TBE) agarose gel using ethidium bromide as a stain. DNA was stored at -20°C until required.

Polymerase chain reaction

The following polymerase chain reaction (PCR) mix was used to amplify the rDNA region: 10 µl 10x PCR buffer, 2 µl 10 mM dNTP mixture (0.2 mM each), 6 µl 25 mM $MgCl_2$, 5 µl primer mix (0.5 µM each), 1.5 µl genomic template, 0.5 µl *Taq* DNA polymerase (2.5 units) and autoclaved distilled water to 100 µl. The conditions applied were: one cycle at 94°C for three min (denaturing), 35 cycles at 94°C for one min (denaturing), 55°C for one min (annealing), 72°C for one min (primer extension), followed by 10 min at 72°C. DNA sequences of the forward primer NC5 (5'-GTA GGT GAA CCT GCG GAA GGA TCA TT-3') and reverse primer NC2 (5'-gg TTA GTT TCT TTT CCT CCG CT-3') correspond to the conserved 3'-5' ends of the ITS1-5.8S rDNA-ITS2 flanking the 18S and 28S regions (Gasser *et al.* 1996). NC2 primer was modified by adding two extra Gs to the 5' end, to assist with TA cloning, and to increase the melting temperature. Samples without DNA were included in each set of PCR reactions for negative control. The PCR products were checked again on agarose gels. The size of PCR fragments were estimated using a DNA ladder.

Cloning and sequencing

Bands were cut from the gel and DNA was extracted from the gel using a Promega Wizard SV Gel and PCR clean-clean up System. The isolated DNA was cloned into *Escherichia coli* (DH5α) using pGEM-T Easy vectors, the 2x Rapid Ligation Buffer (Promega), and pGEM-T Easy Vectors Ligation Reactions (Promega). Transformed cells were selected by overnight incubation at 37°C on LBB/Amp/X-gal/IPTG plates. Single recombinants (clones) were screened for the DNA insert. The clones containing the correct insert were used to inoculate 50 ml of LBB/Amp broth and incubated, while shaking, at 37°C for 12 h. Plasmids were purified using a Plasmid Midi Kit (Quiagen) and sequenced by Macrogen (South Korea) with a universal primer. Sequences from the *T. trichiura* isolated from human hosts were obtained by the UK collaborators in the same way and given to the principal investigator for sequence and phylogenetic analysis.

3.7 Statistical analyses

Statistical analyses were run using the program SPSS 17.0 (SPSS Inc.) except the Generalized Linear Mixed Model which was performed using GenStat (10th edition). Non-parametric tests were used throughout the thesis since most data did not meet the normality assumption for parametric tests. Exact tests were used to increase the reliability of the non-parametric tests. Exact tests enable to make reliable inferences when the data are small, sparse, heavily tied, or unbalanced, by computing exact *p* values. In general, tests were two-tailed and significance levels were set to α=0.05; exceptions to this rule are explained in the pertaining cases.

3.7.1 Parasite morphology

The length and width of the eggs of helminth morpho-species were compared between parasite taxa by using t-tests and between troops by using the nonparametric Kruskal-Wallis test. Nonparametric Mann-Whitney U tests for two independent variables were used for post-hoc tests when significant differences were detected.

3.7.2 Indices of infection (PSR, prevalence, and egg output)

Samples versus individuals

The nonparametric Spearman's Rank Correlation test was used to compare PSR in cumulative faecal samples collected from three baboon troops with known individuals. Helminth and protozoan species richness from samples and individuals were compared with a Mann-

Whitney U test. The same comparison was done for prevalences by using a Wilcoxon signed rank test, a nonparametric test for two related variables. For the rest of the analyses in this study PSR and prevalence were calculated on the basis of number of samples collected per troop, as opposed to number of individuals.

Seasons

Tests on seasonality were done on four troops, namely Buffels Bay, Da Gama Park, Plateau Road, and Tokai for which there were adequate samples in both winter and summer. PSR, prevalence and egg output were compared between the periods of winter 2006, Summer 2006/2007 and winter 2007. Kruskal-Wallis test for several independent samples, the non-parametric equivalent of one-way ANOVA, was used to find possible seasonal effects on protozoan and helminth PSR. Mann-Whitney U tests were used for post-hoc pair-wise comparisons between seasonal PSR. Prevalences between the seasons were compared for each helminth and protozoan taxa with Fisher's Exact tests. These tests are an extension of a Chi-square test for more than two categories (Freeman & Halton 1951) and allow one to make reliable inferences when the sample size is small, heavily tied, or unbalanced. Analyses on seasonality of egg output could be done only on two helminth species, *Trichuris* sp. and *Oesophagostomum* sp., because of the sample sizes not being large enough for the other helminth taxa. The troops analyzed were Plateau Road and Da Gama Park. Buffels Bay and Tokai troops were not included in this analysis, because not enough data were available for the winter seasons. Only positive samples were used and values of eggs/g were first log (n+1)-transformed, in an attempt to obtain a normal distribution. However, since this was not achieved, a Kruskal-Wallis H test was used to uncover seasonal effects on egg output, and Mann-Whitney U tests were performed as post-hoc tests. Egg emission was then compared between parasite taxa, independently from the season, with a Kruskal-Wallis test. Prevalences of helminth and protozoan taxa were compared with other studies done on other chacma baboon populations in South Africa using Chi square tests.

Comparison with other studies

To avoid a potential confounding bias due to seasonal and year differences in parasite infections, only data of the winter season 2007 were used for calculation of PSR (n=271). The only exception was represented by the Tokai troop, for which data of the two winter seasons 2006 and 2007 were pooled in order to increase the otherwise too small sample size.

Winter 2007 were chosen above summer 2006/2007 data because sample collection took place only in winter for Cape Point and Kanonkop troops.

Parasite species diversity and prevalences found in the Cape Peninsula baboons were compared to the same infection indices found in previous studies on chacma baboon in South African localities. Only helminth taxa identified to the genus level were included in the analysis, except *Ascaris* sp., which was not included, being rarely found in chacma baboon. Prevalences of helminth taxa were compared to nine other localities using Chi-square tests of independence, while prevalences of protozoan taxa were compared to six other localities. The names of these locations are written in bold in Appendix A. The chacma baboon is also found in Zimbabwe and Namibia, but only South African localities were compared.

Age and sex

The troops Plateau Road, Da Gama Park, and Buffels Bay were used for comparisons between host sex classes (male and female). For age class (juveniles and adults) comparisons, analyses included Plateau Road, Da Gama Park, and Tokai troops. A Mann-Whitney U test was performed for comparisons involving PSR, while prevalences were compared between groups using a Fisher's Exact test.

Reproductive status

Adult females of different reproductive status were pooled across all six study troops to obtain an adequate sample size. Prevalences were compared using a Fisher's Exact test. Only *Trichuris* sp. and *Oesophagostomum* sp. provided sufficient positive samples to allow for a statistical comparison of egg output. Similarly, only the protozoa *Balantidium coli*, *Entamoeba coli*, *E. histolytica/dispar*, and *E. chattoni* were present in large enough numbers to allow for an analysis (Kruskal-Wallis test) of reproductive status and protozoa prevalence/PSR. It was not possible to investigate variation in egg output with reproductive status in the same individual due to small sample sizes.

Social status

Only adult females of known rank, belonging to the troops Buffels Bay, Da Gama Park, and Plateau Road were used in this analysis; data from the three troops were pooled. Furthermore, only individuals for whom at least three repeat samples (the minimum sample size for a reliable estimate of individual PSR were included in the analyses. PSR was compared between rank categories (low, medium, and high) using a Kruskal-Wallis test and Mann-Whitney U test for post hoc comparisons. Prevalences were compared with a Fisher's Exact test; the taxa *Trichuris* sp., *Oesophagostomum* sp., *B. coli*, and *E. coli* could not be compared, as they were present in all individuals analyzed. To compare egg outputs, a Generalized Linear Mixed Model (GLMM) was used, first to analyse the effects of troop and season on mean egg output of each parasite taxon (Table 3.5). GLMMs can be used when multivariate analyses involve repeated sampling of groups and individuals. Due to the lack of significant interactions, data from different troops and seasons were pooled to create an adequate sample size and comparisons between social status categories were then done using a Fisher's Exact test.

Table 3.5 F values for main effects and interactions generated by GLMM for mean egg/cyst output; *p≤ 0.05.

Parasite taxa	Season	Troop	Season * Troop
Trichuris sp.	2.64	2.80*	0.61
Oesophagostomum sp.	0.03	0.17	0.57
Trichostrongylus sp.	0.04	0.27	0.42
Physaloptera sp.	0.02	0.21	0.31
Ascaris sp.	2.27	0.04	0.00
Balantidium coli	0.01	0.31	0.20
Entamoeba coli	0.05	0.05	0.06
E. histolytica/dispar	0.00	0.00	0.00
E. chattoni	0.03	0.02	0.10
E. hartmanni	0.04	0.09	0.02
Iodamoeba bütschlii	0.26	0.07	0.10
Chilomastix mesnili	0.10	0.13	0.09

Comparisons between troops

In order to detect variations of PSR between the study troops, Kruskal-Wallis tests and Mann-Whitney U tests were performed. The prevalences of each parasite taxa were compared across troops with a Chi square test. The prevalences were also compared between each troop separately using Mann-Whitney U tests. Because multiple comparisons were run, I corrected for multiple tests using the Benjamini and Yekutieli modified False Discovery Rate method, which has been shown to be a meaningful experiment-wise correction for multiple pairwise tests that reduces Type I error while maintaining statistical power (Narum 2006). Covariance between ecological variables and troop attributes were tested using one-tailed Spearman's Rank Correlations. Covariance between nematode prevalences was tested with the same method, and so was the covariance between PSR and taxa prevalences and both ecological variables and troop attributes. Since these were also multiple comparisons, the Benjamini and Yekutieli modified False Discovery Rate method was also applied.

3.7.3 Molecular analyses: sequence and phylogenetic analysis

Vector sequences were trimmed from the nucleotide sequences in BioEdit (Ibis Biosciences). Clones that shared 100% similarity were considered to be identical and were merged. Nucleotide sequences for the ITS1-5.8S rDNA-ITS2 regions isolated in this study were submitted to GenBank, and their accession numbers are listed in Table 3.6.

Table 3.6 Genbank Accession Numbers of sequences identified in this study.

Genbank Accession Number	Species	Host	Individual
GQ301553	*Trichuris papionis* DGI	*Papio ursinus*	Zoey, Da Gama Park Troop (DG)
GQ301552	*Trichuris papionis* DGII	*Papio ursinus*	Sara, Da Gama Park Troop (DG)
GQ301551	*Trichuris papionis* DGIII	*Papio ursinus*	Dara, Da Gama Park Troop (DG)
GQ301554	*Trichuris_trichiura*_host_ *Papio ursinus*	*Papio ursinus*	Identical sequences from two baboons in the Cape Peninsula Troops Cape Point (CP) and Groot Olifantsbos (GOB)
GQ301555	*Trichuris trichiura*	*Homo sapiens*	Isolated from patients in the Cameroon

The nucleotide sequences of *Trichuris* clones identified in baboons and human patients were aligned using PRANK (Löytynoja & Goldman 2005) with other full-length ITS1-5.8S rDNA-ITS2 sequences (Table 3.7). Alignments were submitted to Phylogeny.fr interface server (Dereeper *et al.* 2008), and phylogenetic trees were inferred using maximum likelihood in PhyML with the HKY85 substitution model (Guindon & Gascuel 2003). The approximate likelihood ratio test was used to assess the robustness of the phylograms (Anisimova & Gascuel 2006). Trees were viewed using Treedyn (Chevenet *et al*. 2006).

Table 3.7 Genbank Accession Numbers for full-length ITS1-5.8S rDNA-ITS2 regions used in this study.

Genbank Accession Number	Species	Host
AJ299407	*Trichuris muris*	Murid hosts
AM234616	*Trichuris vulpis*	*Canis lupus familiaris*
AJ783398 AM229670 AJ249966	*Trichuris suis*	*Sus scrofa scrofa* *Sus scrofa sp.* *Sus scrofa domestica*
FM991955	*Trichuris trichiura*	*Nomascus gabriellae*
AB367795	*Trichuris discolor*	*Capricornis crispus*
AB367794	*Trichuris discolor*	*Capricornis crispus*
AJ489248	*Trichuris skrjabini*	*Capra hircus*

CHAPTER FOUR

GASTROINTESTINAL PARASITES OF THE CAPE PENINSULA BABOON POPULATION

4.1 Parasites identified

4.1.1 Helminths

Seven different helminth taxa, all nematodes, were recovered from 616 faecal samples collected from six baboon troops within the Cape Peninsula (Table 4.1). One of the seven taxa, *Trichuris* sp., belonged to the class Enoplea while the other six taxa belonged to the class Chromadorea. *Trichuris* sp. was identified based on the size (59.1 ± 4.2 × 27.7 ± 2.0 µm) and morphology of the eggs (barrel shape, yellow-brown coloration, bipolar plugs, Figure 4.1.A) and from adult specimens found during opportunistic necropsies of baboon gastrointestinal tracts (*n*=5). Eggs of *Trichuris* sp. were found in faeces of individuals in all six troops.

Three morpho-species belonging to the polyphyletic group of the "strongylids", which comprises the orders Rhabditida and Tylenchida (Strongylida), were found. All the species were from the order Rhabditida, the first of which, *Oesophagostomum* sp., was identified based on egg size and morphology (elliptical, unlarvated, Figure 4.1.B), cultured larvae (Figure 4.1.H), and adult specimens from opportunistic necropsies (*n*=5). Eggs were found in faeces of individuals in all six troops, and measured 69.9 ± 4.0 × 44.2 ± 2.1 µm. Eggs of the second strongylid, *Trichostrongylus* sp., were found in five of the six troops; they were identified based on their morphology (usually asymmetrical in shape with one side slightly flattened toward the end, usually unlarvated, Figure 4.1.C) and size, which was 83.4 ± 4.7 × 46.7 ± 2.4 µm. The third Rhabditida was an unidentified hookworm morpho-type; its eggs were similar to *Oesophagostomum* sp. eggs (Figure 4.1.D) and measured 69.7 ± 0.2 × 41.9 ± 0.1 µm. They were significantly smaller than *Oesophagostomum* sp. eggs in width (t=2.395,

Table 4.1 Classification of the gastrointestinal fauna found in the study animals. Helminth taxonomy follows Benson *et al.* (2000) and Wheeler *et al.* (2000). Protozoa taxonomy follows Brands, S. J. (comp.) (1989-present)

Parasite morpho-species	Phylum	Class	Order (Suborder)	(Superfamily) Family
Trichuris sp.	Nematoda	Enoplea	Trichocephalida	(Trichuroidea) Trichuridae
Oesophagostomum sp.	Nematoda	Chromadorea	Rhabditida (Strongylida)	(Strongyloidea) Chabertiidae
Trichostrongylus sp.	Nematoda	Chromadorea	Rhabditida (Strongylida)	(Trichostrongyloidea) Trichostrongylidae
Physaloptera sp.	Nematoda	Chromadorea	Spirurida	(Physalopteroidea) Physalopteridae
Ascaris sp.	Nematoda	Chromadorea	Ascaridida	(Ascaridoidea) Ascarididae
Hookworm type	Nematoda	Chromadorea	Rhabditida (Strongylida)	(Ancylostomatoidea) Ancylostomatidae
Unidentified spirurid	Nematoda	Chromadorea	Spirurida	unknown
Balantidium coli	Ciliophora	Litostomatea	Vestibuliferida	Balantidiidae
Entamoeba coli	Amoebozoa	Archamoebea	Pelobiontida	Entamoebidae
E. histolytica/dispar	Amoebozoa	Archamoebea	Pelobiontida	Entamoebidae
E. chattoni	Amoebozoa	Archamoebea	Pelobiontida	Entamoebidae
E. hartmanni	Amoebozoa	Archamoebea	Pelobiontida	Entamoebidae
Iodamoeba buetschlii	Amoebozoa	Archamoebea	Pelobiontida	Entamoebidae
Endolimax nana	Amoebozoa	Archamoebea	Mastigamoebida	Mastigamoebidae
Chilomastix mesnili	Metamonada	Retortamonadea	Retortamonadida	Retortamonadidae

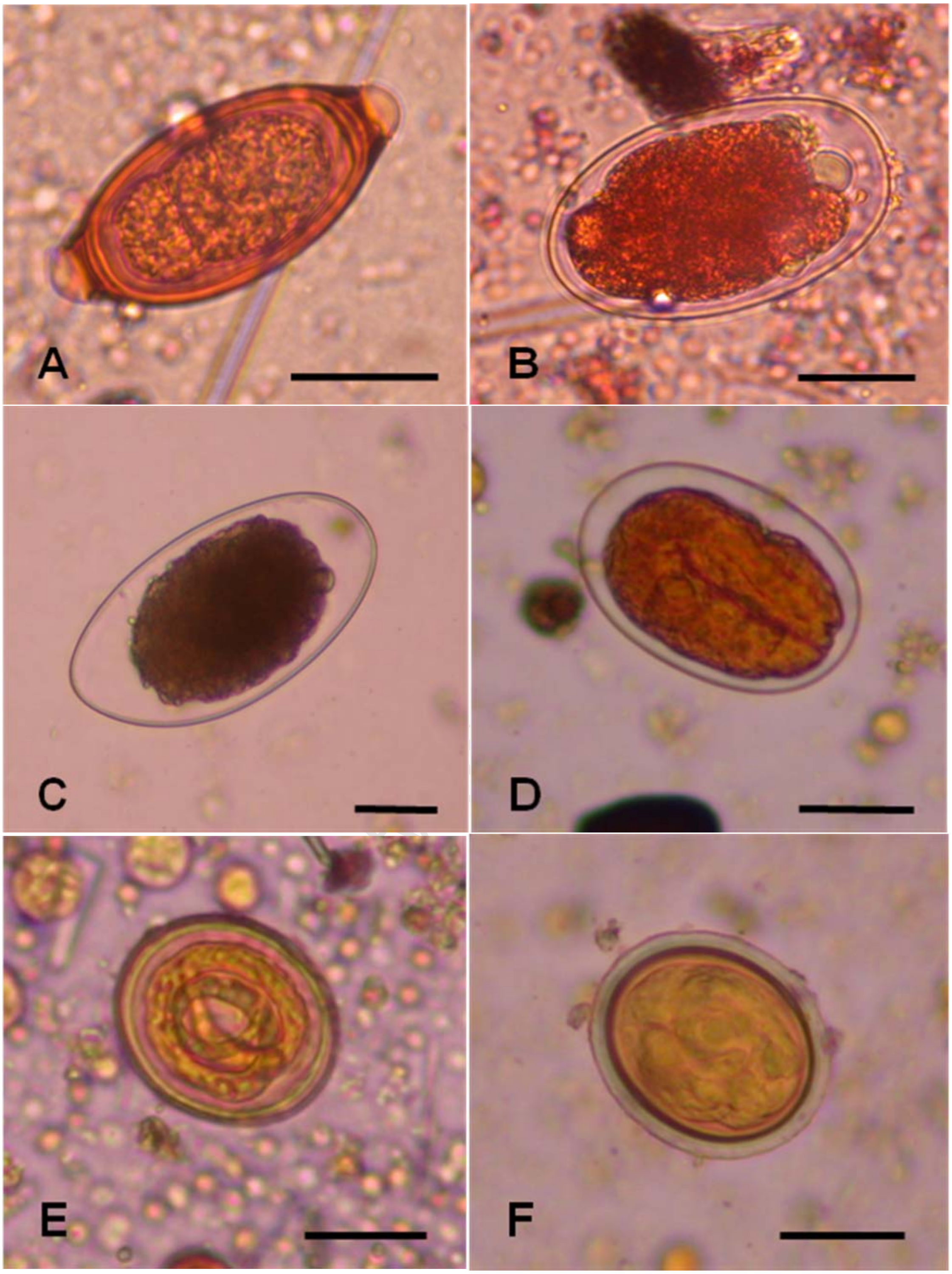


Figure 4.1. (A-H) Light microscope pictures of helminth eggs (recovered from baboon faecal samples) and larvae (cultured from eggs). A. *Trichuris* sp., B. *Oesophagostomum* sp., C. *Trichostrongylus* sp., D. Hookworm type, E. *Ascaris* sp., embryonated, F. *Physaloptera* sp., G. Spirurid, H. Larva of *Oesophagostomum* sp. Scale bar = 25 µm.

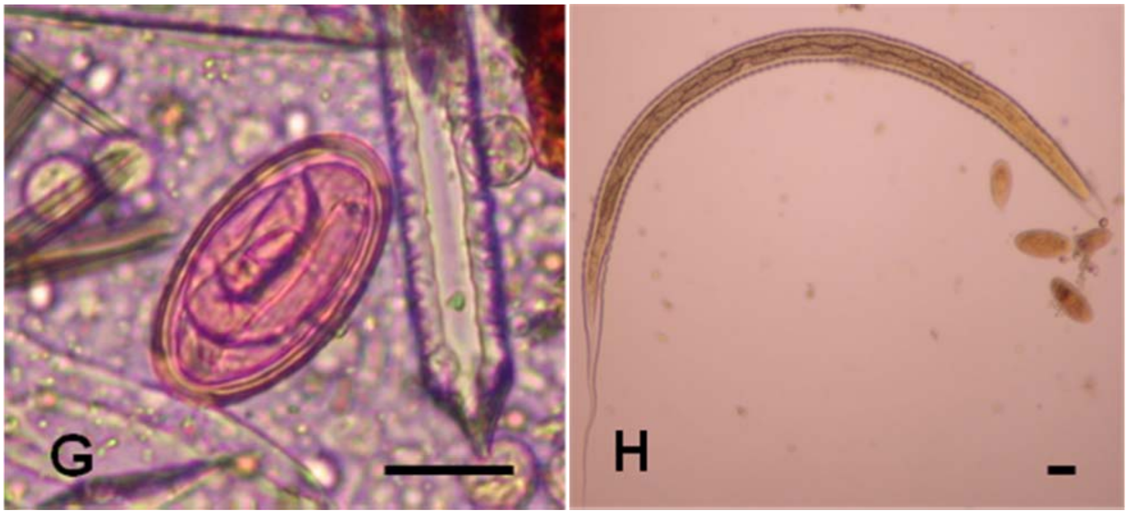


Figure 4.1. (A-H) continued

df=816, p=0.017) but not in length (t=1.919, df=816, p=0.062). Coprocultures on this morpho-type could not be performed, due to the small number of eggs recovered per faeces. The only morpho-species belonging to the order Ascaridida, *Ascaris* sp., was identified on the basis of egg morphology. Both fertile ova (oval in shape, with a thick, smooth shell covered by a brown mammilated coat, Figure 4.1.E) and infertile ones (longer and narrower and with a thinner egg shell and albuminous coat) were recovered from individuals sampled in five of the six troops. Eggs measured 61.7 ± 2.6 × 49.9 ± 2.5 µm. Of the two recovered morpho-types belonging to the order Spirurida, one was identified as *Physaloptera* sp. through egg size and morphology (oval to spherical, thick shelled, surrounded by a frilly outer coat, Figure 4.1.F) and adult specimens found through opportunistic necropsies (*n*=5). The eggs measured 50.6 ± 3.0 × 38.7 ± 2.3 µm. The other Spirurida helminth was recovered only from faeces of one baboon troop and could not be identified further (Figure 4.1.G). Eggs of this morpho-type measured 60.8 ± 1.4 × 32.2 ± 0.9 µm. Larvae were also present in very few (*n*<10) samples. However, given the low number found and the uncertain identification and origin, these larvae were not included in further analyses.

The descriptive statistics of length and width for eggs of each parasite morpho-species for all troops pooled are summarized in Table 4.2. Nematode larvae are not included in the table because they were identified on the basis of their morphology and not their size. The results of statistical comparisons of egg sizes between baboon troops are showed in Appendix C. Sizes found in the literature are presented in Appendix D. Length and width of parasite taxa varied significantly between troops in the case of *Ascaris* sp. and *Physaloptera* sp.

Table 4.2 Descriptive statistics for eggs of six morpho-species of parasites. L=length, W=width. Numbers in italic represent the number (*n*) of eggs measured. IQR=interquartile range. Mean, median, minimum, maximum, and IQR are in µm.

	All troops		Buffels Bay		Cape Point		Da Gama Park		Kanonkop		Plateau Road		Tokai	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
***Oesophagostomum* sp.**	*n=809*	*n=809*	*n=119*	*n=119*	*n=60*	*n=60*	*n=248*	*n=248*	*n=164*	*n=164*	*n=183*	*n=183*	*n=35*	*n=35*
Mean	69.9	44.2	69.9	43.9	70.0	44.2	70.1	44.0	69.7	44.2	69.8	44.4	69.5	44.2
Std. Dev.	4.0	2.1	4.1	1.9	4.3	2.0	4.1	2.2	4.1	2.0	3.6	2.1	4.2	2.0
Median	69.6	44.5	69.6	44.5	69.6	44.5	69.6	44.5	69.3	44.5	69.3	44.5	69.2	44.5
Minimum	56.7	37.1	58.8	37.5	56.9	37.1	56.8	37.1	56.7	37.5	56.8	38.4	58.8	37.5
Maximum	80.5	54.3	80.5	49.5	80.1	49.3	80.5	54.3	80.5	49.5	80.4	51.2	80.5	47.7
IQR	4.8	2.0	4.3	1.5	5.7	1.8	5.1	1.6	4.8	2.4	4.7	2.4	5.3	2.1
***Trichostrongylus* sp.**	*n=65*	*n=65*	*n=12*	*n=12*	*n=4*	*n=4*	*n=6*	*n=6*	*n=13*	*n=13*	*n=22*	*n=22*	*n=8*	*n=8*
Mean	83.4	46.7	81.3	46.2	87.4	47.5	83.5	44.2	83.2	47.4	82.7	47.1	87.1	46.2
Std. Dev.	4.7	2.4	3.8	2.0	1.2	2.1	7.5	1.9	3.9	2.3	4.6	2.6	3.4	2.4
Median	83.9	46.7	80.8	45.6	87.2	47.5	81.8	43.5	82.8	48.0	83.4	48.1	86.8	45.3
Minimum	75.7	42.9	75.7	42.9	86.4	45.6	76.7	43.2	78.9	43.3	76.4	42.9	82.8	43.4
Maximum	92.4	51.9	88.8	49.5	88.8	49.5	92.4	48.0	91.2	50.9	91.4	51.9	91.3	50.3
IQR	7.3	4.1	6.0	3.4	2.2	3.8	14.7	1.5	6.7	3.8	7.7	4.5	6.8	4.1
***Physaloptera* sp.**	*n=39*	*n=39*	*n=0*	*n=0*	*n=1*	*n=1*	*n=4*	*n=4*	*n=3*	*n=3*	*n=31*	*n=31*	*n=0*	*n=0*
Mean	50.6	38.7					53.8	39.7	52.9	40.7	50.0	38.3		
Std. Dev.	3.0	2.3					1.9	0.3	0.2	0.1	3.0	2.4		
Median	51.0	39.4					54.5	39.7	52.8	40.8	51.0	39.4		
Minimum	43.0	31.5					51.0	39.4	52.7	40.6	43.0	31.5		
Maximum	55.2	43.0					55.1	40.0	53.1	40.8	55.2	43.0		
IQR	5.5	2.6					3.2	0.5	n/a	n/a	3.9	2.4		
***Ascaris* sp.**	*n=138*	*n=138*	*n=0*	*n=0*	*n=20*	*n=20*	*n=29*	*n=29*	*n=41*	*n=41*	*n=32*	*n=32*	*n=16*	*n=16*
Mean	61.7	49.9			61.1	48.9	63.5	51.8	61.0	50.7	62.1	48.0	60.5	51.0
Std. Dev.	2.6	2.5			2.1	2.5	3.7	2.9	1.7	2.0	2.6	2.3	0.8	0.9
Median	61.1	50.4			60.3	49.9	63.8	51.6	60.7	50.9	62.9	48.4	60.6	51.0
Minimum	57.5	43.2			58.7	44.7	58.8	44.7	58.7	44.7	57.5	43.2	58.9	49.8
Maximum	71.6	54.3			64.9	52.2	71.6	54.3	66.7	54.3	65.3	51.4	61.5	53.0
IQR	3.9	2.7			4.4	4.2	4.7	2.1	1.5	1.6	5.1	3.8	1.3	1.5

For *Physaloptera* sp. morpho-type the maximum variance was less than what has been reported in the literature. In particular, average length and width were within the range reported by Meade (1984; length: 28.3-56.5 µm; width: 17.9-38.5 µm) and all *Physaloptera* sp. in my study were thus grouped as one species. Average length for *Ascaris* sp. was smaller than values reported in the literature (Brack 1987: length: 65.0-75.0 µm; width: 35.0-50.0 µm), but they were nevertheless grouped as one *Ascaris* sp. since egg size for this taxon is known to vary greatly in accordance with the development stage of the egg.

Information on the ecology of the different parasites reported above was compiled from the literature and is presented in Appendix D. This synthesis includes information on life cycle, transmission mode, host specificity and other parameters of importance relevant to obtaining an understanding of the mechanisms of parasite infection.

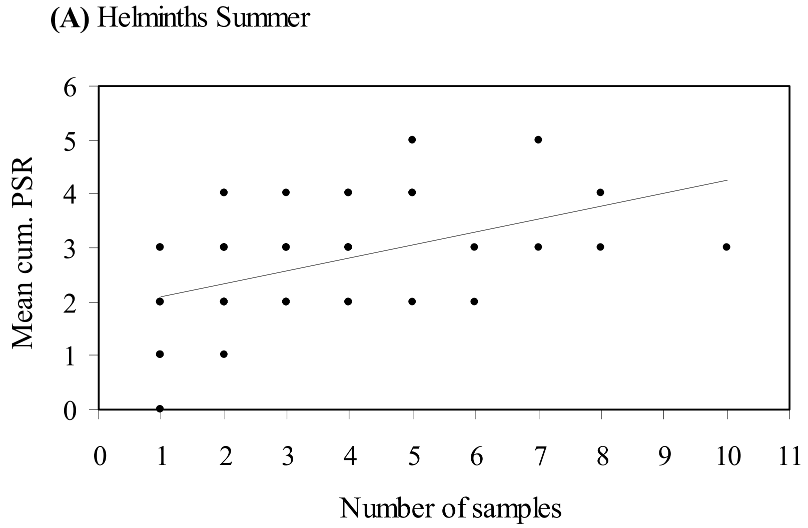
4.1.2 Protozoa

Cysts of one ciliate, six amoebae, and one flagellate were identified from 616 faecal samples collected from animals in six Cape Peninsula troops (Table 4.1). *Balantidium coli* cysts, the ciliate protozoa, were recognized on the basis of their spherical shape and large size (50-70 µm in diameter). *Entamoeba coli* cysts are spherical and large (10-35 µm in diameter); several of the eight nuclei are readily visible. *Entamoeba histolytica/dispar* was reported in this way because cysts of the pathogenic *E. histolytica* are indistinguishable from the non-pathogenic *E. dispar*. Both cysts are spherical, measure 10 to 20 µm in diameter and contain one or two to four nuclei; they are very similar to immature *E. coli* cysts. *Entamoeba chattoni* cysts are also spherical (9-18 µm) and usually have one nucleus; their cytoplasm contains small visible inclusions. Mature cysts of *Entamoeba hartmanni* (5-10 µm) have four nuclei and elongated chromatoid bodies with rounded ends. *Iodamoeba butschlii* cysts (5-20 µm) are characterized by one nucleus and a large glycogen vacuole that stains dark brown with iodine. *Endolimax nana* cysts are small (5-10 µm), spherical or ovoid in shape, and contain four pinpoint nuclei. *Chilomastix mesnili* is a flagellate and its cysts are uninucleate and have a typical lemon-shaped appearance (6-10 µm long). Information on the ecology of the protozoa collected can be found in Appendix D.

4.2 Number of samples versus number of individuals

4.2.1 Cumulative number of parasite species per individual

Figures 4.2.A and B present scatter plots of the number of intestinal helminth and protozoa species present in each individual from one of three troops (Buffels Bay, Da Gama Park, and Plateau Road) in relation to the number of faecal samples examined for that individual. The data used in these analyses were from the summer season only.



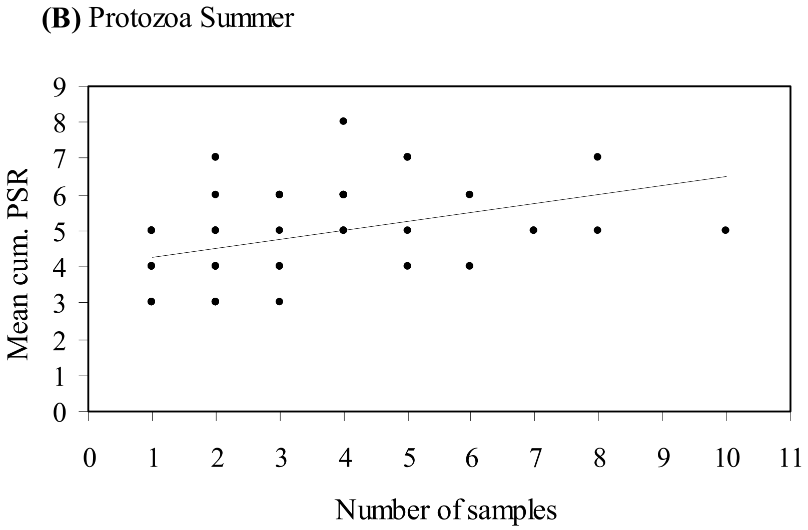
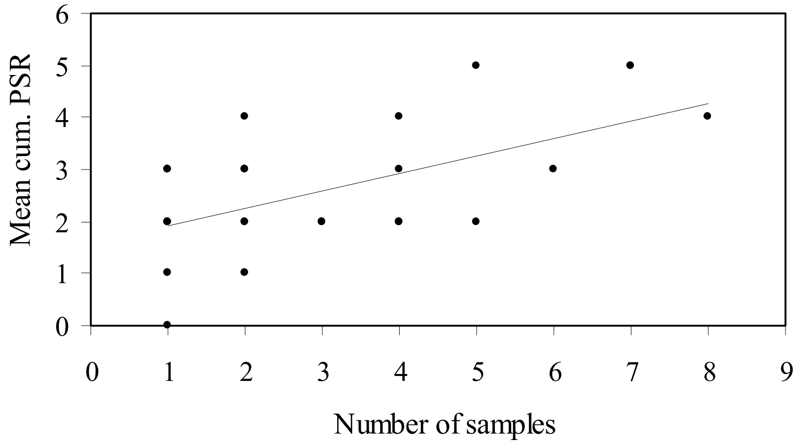


Figure 4.2. (A-B) Scatter plots of cumulative (cum.) number of helminth (A) and protozoan (B) species detected for each individual against number of samples examined for that individual in summer.

Samples collected in winter were analyzed separately and are shown in Figures 4.3.A and B.

A significant correlation was detected between the number of samples analyzed per individual in summer and the cumulative number of helminth (Spearman rank correlation: r_s=0.544; *n*=52, p<0.001) and protozoan (r_s=0.480; *n*=52, p<0.001) species. The relationship between the number of samples and the mean cumulative species richness was not significant when the number of samples analyzed per individual was equal to or greater than three samples (Helminths: r_s=0.343; *n*=26, p=0.086; Protozoa: r_s=0.052; *n*=26, p=0.799). Using this criterion, I thus restricted my sample size to the 26 individuals for which I had three or more samples for all analyses of host individual traits and parasite infection levels.

(A) Helminths Winter



(B) Protozoa Winter

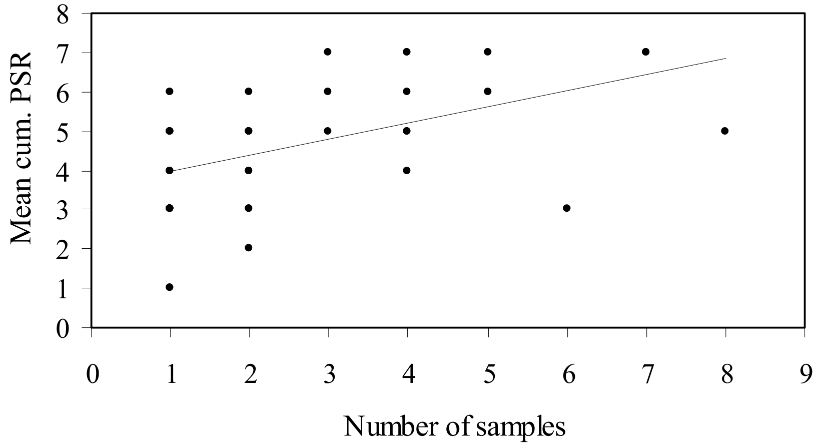


Figure 4.3. (A-B) Scatter plots of cumulative (cum.) number of helminth (A) and protozoan (B) species detected for each individual against number of samples examined for that individual in winter.

Similarly, a significant correlation was found for winter data between the number of samples analyzed per individual and cumulative number of helminth (r_s=0.414; *n*=39, p=0.009) and protozoa (r_s=0.551; *n*=39, p<0.001) species detected. The relationship between these two variables was not significant when only individuals from which five or more samples were obtained were included in the analysis (Helminths: r_s=0.281; *n*=6, p=0.589; Protozoa: r_s=-0.094; *n*=6, p=0.860). Using this cut-off number for individual level analyses the final sample size was only six individuals, which was considered too small for further analyses. Individual variation in parasite prevalence and parasite species richness (PSR) were thus restricted to data obtained during the summer months.

4.2.2 PSR and prevalence based on samples versus individuals

Data from faecal samples collected during summer were used to compare PSR and prevalence calculated from both samples and individuals. The mean PSR of helminths calculated using sample data was 1.45 (*n*=139 samples) which was significantly lower (Mann-Whitney U test: U=523.000; *n*=165, p<0.001) than mean PSR of 3.08 (*n*=26 individuals) calculated using individuals as data points. The mean PSR of protozoa calculated for samples was 3.27 (*n*=139 samples) which was significantly lower (Mann-Whitney U test: U=380.500; *n*=165, p<0.001) than the mean PSR of 5.46 calculated using individuals (*n*=26 individuals).

Similarly, the prevalences calculated using data from individuals were significantly higher than prevalences calculated using samples (Wilcoxon signed rank test: Z=-3.409; *n*=15, p=0.001) (Figure 4.4).

All subsequent analyses on indices of infection are based on the number of samples, with only a few highlighted exceptions; it is important to bear this in mind, especially when comparing results to other studies, where some authors report true prevalences and others report the percentage of samples found to be positive (Mühlenbein 2005). Prevalence values reported in the following analyses should therefore be viewed as an index of prevalence.

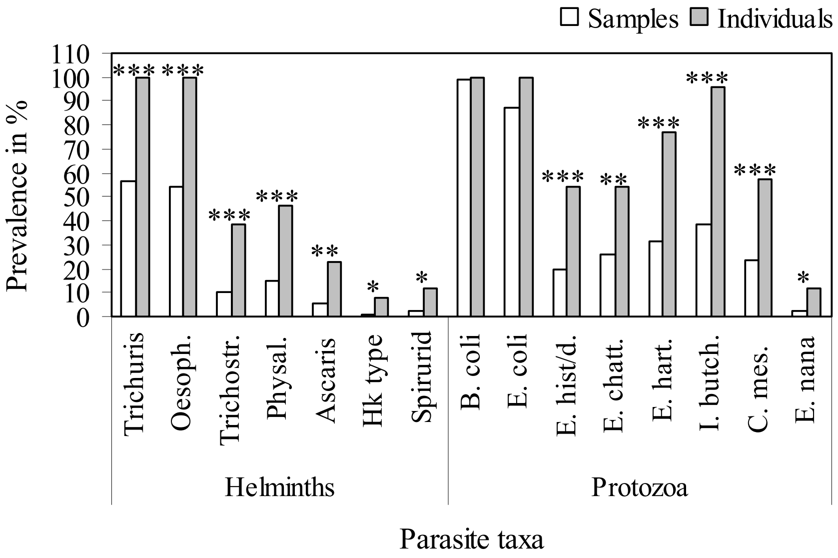


Figure 4.4 Prevalences for species of helminths and protozoa calculated from samples and from individuals. Asterisks indicate statistical differences: Mann-Whitney U test: *p≤ 0.05, **p≤ 0.01, ***p≤ 0.001. (Trichuris=*Trichuris* sp., Oesoph.=*Oesophagostomum* sp., Trichostr.=*Trichostrongylus* sp., Physal.=*Physaloptera* sp., Ascaris=*Ascaris* sp., Hk =hookworm, B. coli=*Balantidium coli*, E. coli=*Entamoeba coli*, E. hist/d.=*E. histolytica/dispar*, E. chatt.=*E. chattoni*, E. hart.= *E. hartmanni*, I. butch.=*Iodamoeba butschlii*, C. mesn.=*Chilomastix mesnili*; E. nana=*Endolimax nana*).

4.3 Seasonality

Figure 4.5 shows the monthly total rainfall and average minimum and maximum temperatures reported in the Cape Peninsula during the study period. Rainfall was reported throughout the year, but peaked between May and August (the austral winter) when ambient temperatures were lowest. Rainfall in Tokai was significantly higher than in the rest of the southern Peninsula (Wilcoxon: *n*=24, Z=-4.257, p<0.001).

Maximum temperature did not differ between the two winter seasons (May to August) during which data was collected (2006 and 2007; T-test for independent means: t=-0.376, df=717, p=0.707), but did differ significantly between winter 2006 and summer 2006-2007 (T-test for independent means: t=-21.957, df=686, p<0.001) and between summer 2006-2007 and winter 2007 (T-test for independent means: t=22.818, df=663, p<0.001). The same pattern was found for minimum temperature, with no significant difference between winter 2006 and winter 2007 (T-test for independent means: t=-0.809, df=714, p=0.419) but significant difference between winter 2006 and summer 2006-2007 (T-test for independent means: t=-

27.671, df=645, p<0.001) and between summer 2006-2007 and winter 2007 (T-test for independent means: t=25.604, df=648, p<0.001).

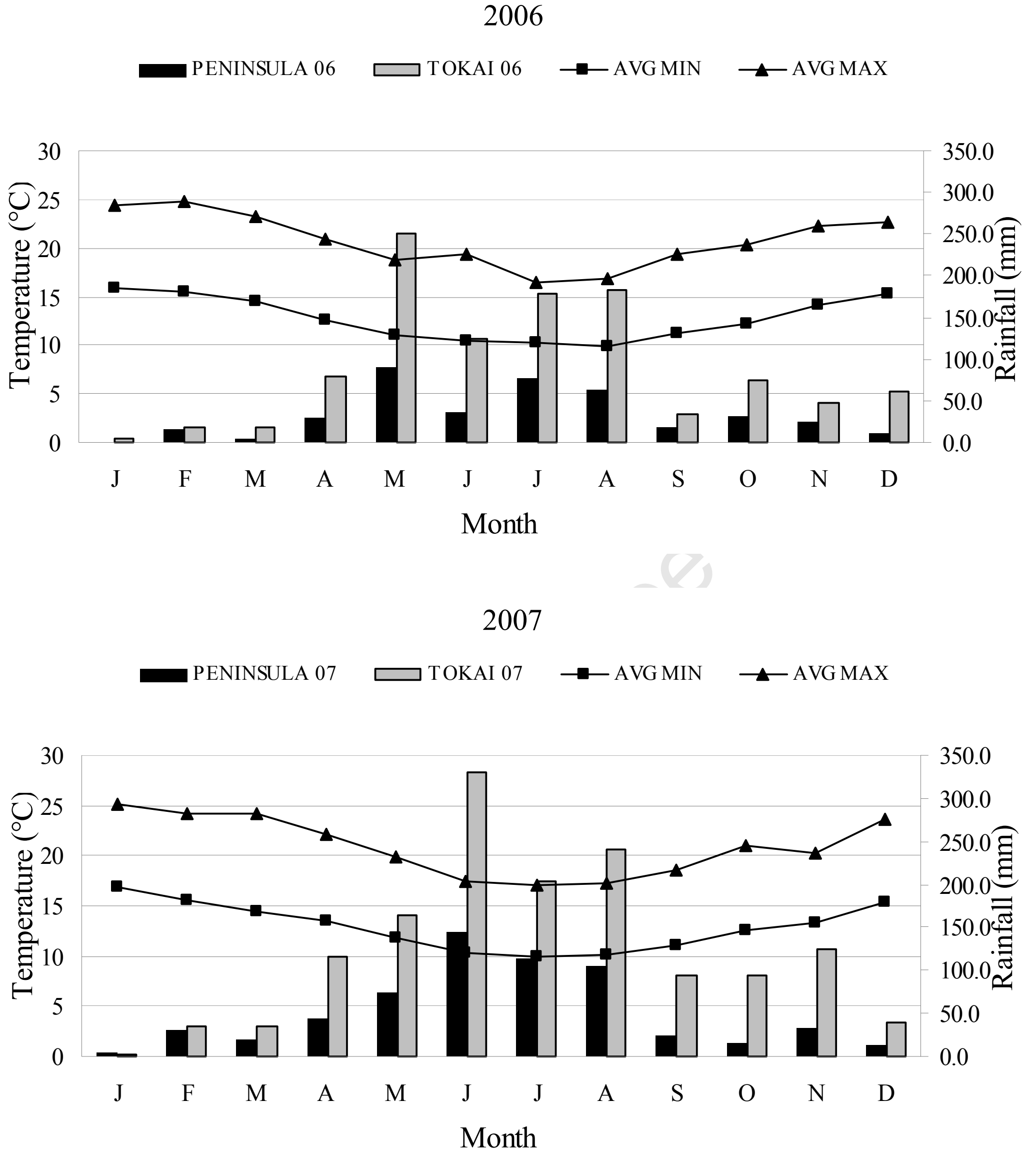


Figure 4.5 Monthly rainfall and mean daily minimum and maximum temperature (°C) for 2006 and 2007.

More days with rain were reported in both winters for both the Cape Peninsula (47 and 50 for winter 2006 and winter 2007, respectively) and Tokai (42 and 43) locations than in summer 2006-2007 (Cape Peninsula: 21; Tokai: 16). Total rainfall was also higher in the winter seasons for both the Cape Peninsula (267 mm and 435 mm for winter 2006 and winter 2007, respectively) and Tokai (738 mm and 940 mm) locations than in summer 2006-2007 (Cape

Peninsula: 72 mm; Tokai: 145 mm). Interestingly, while maximum and minimum temperatures did not differ between the 2006 and 2007 winter seasons, total rainfall was much higher for both the Peninsula locations in winter 2007 (Cape Peninsula: 435 mm; Tokai: 940 mm) compared to total rainfall in winter 2006 (Cape Peninsula: 267 mm; Tokai: 738 mm).

Sample sizes varied somewhat between seasons across troops. Plateau Road provided the best data set, with a large number of samples evenly distributed across the three sample periods (*n*=60, 51, and 83 for winter 2006, summer 2006/2007 and winter 2007, respectively). For Da Gama Park, a slightly larger number of samples was collected in summer (*n*=11, 62, and 41 for winter 2006, summer 2006/2007 and winter 2007, respectively). The same pattern was more accentuated in Tokai troop, with *n*=18, 50, and four samples (winter 2006, summer 2006/2007 and winter 2007, respectively). In Buffels Bay, samples were only collected in two seasons, summer 2006/2007 (*n*=26) and winter 2007 (*n*=36).

4.3.1 Parasite species richness

The Kruskal-Wallis H tests uncovered several significant variations in helminth and protozoan PSR between seasons (Figure 4.6.A-H). There was no difference in helminth and protozoan diversity across seasons for individuals in the Buffels Bay troop (Kruskal-Wallis H for helminths: Chi-square=2.927; *n*=62, df=1, p=0.087; Kruskal-Wallis H for protozoa: Chi-square=1.272; *n*=62, df=1, p=0.259), with all parasite species present in both seasons (Figure 4.6.A-B). Protozoan diversity did not vary significantly across seasons for individuals in the Da Gama Park troop (Kruskal-Wallis H: Chi-square=4.180; *n*=114, df=2, p=0.124), but helminth diversity did (Kruskal-Wallis H: Chi-square=46.065; *n*=114, df=2, p<0.001; Figure 4.6.C-D). Post-hoc tests revealed that mean helminth PSR in this troop was significantly lower in summer compared to both winter seasons (Mann-Whitney U for summer 2006/2007 and winter 2006: U=134.500; *n*=73, p=0.001; Mann-Whitney U for summer 2006/2007 and winter 2007: U=363.500; *n*=103, p<0.001; see Figure 4.6). The same parasite taxa were recovered in all seasons, except for hookworm type (helminth) and *Endolimax nana* (protozoan), which were only recovered in winter 2007.

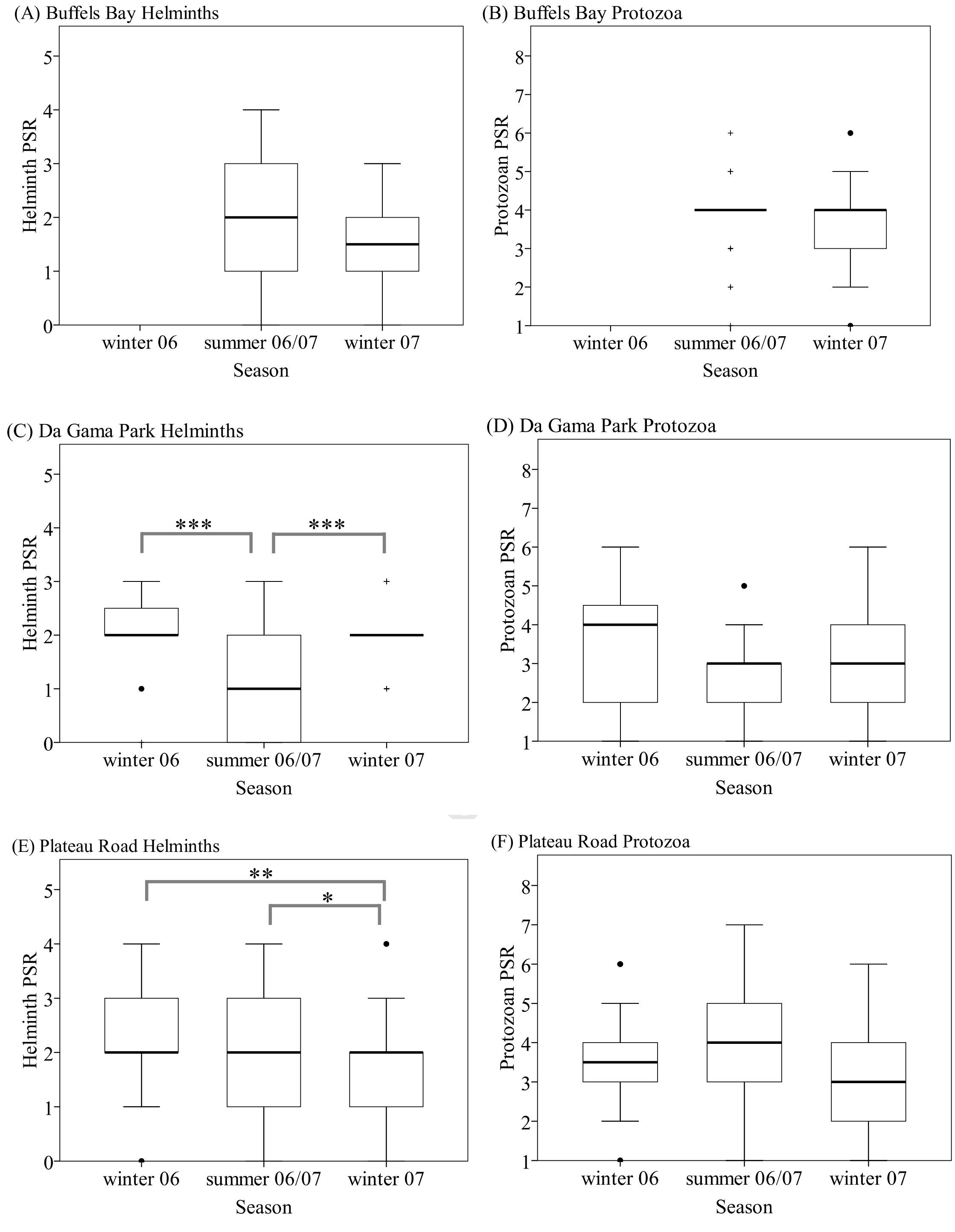


Figure 4.6.(A-H) Parasite species richness in winter and summer across two years in four Cape Peninsula baboon troops. The boxes show the interquartile ranges, bold horizontal bars show the median. The ends of the 'whiskers' represent the largest and smallest values that are not outliers. The circles represent outliers. Asterisks indicate statistical differences: Mann-Whitney U test: *p≤ 0.05, **p≤ 0.01, ***p≤ 0.001.

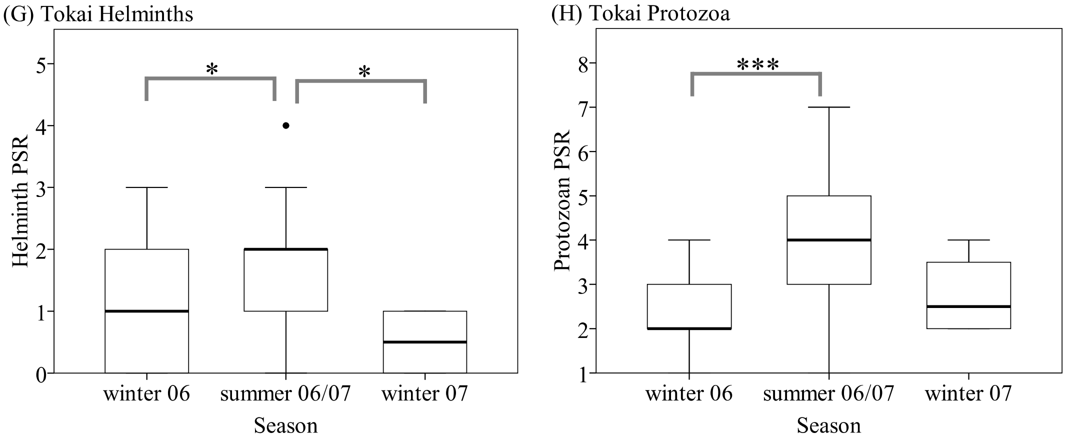


Figure 4.6.(A-H) continued

Plateau Road's helminth diversity showed significant variation across seasons (Kruskal-Wallis H: Chi-square=8.453; *n*=194, df=2, p=0.015). Post-hoc tests showed that helminth diversity did not differ between winter and summer (Mann-Whitney U for summer 2006/2007 and winter 2006: U=1312.500; *n*=111, p=0.175; Mann-Whitney U for summer 2006/2007 and winter 2007: U=1901.500; *n*=134, p=0.304), but varied between the two winter seasons, with helminth diversity being significantly higher in winter 2006 compared to winter 2007 (Mann-Whitney: U=1790.000; *n*=143, p=0.002; Figure 4.6.E-F). Hookworm type was only found in winter 2006, and the unidentified spirurid was only found in winter 2006 and summer 2006/2007. No seasonal difference in PSR was found for protozoa (Kruskal-Wallis H: Chi-square=4.656; *n*=194, df=2, p=0.097). The protozoan *E. nana* was only found in summer 2006/2007 in this troop. In the Tokai troop, significant seasonal differences were found for both helminth and protozoan PSR (Kruskal-Wallis H for helminths: Chi-square=11.342; *n*=72, df=2, p=0.003; Kruskal-Wallis H for protozoa: Chi-square=17.638; *n*=72, df=2, p<0.001). Helminth diversity was significantly lower in the two winter seasons than in summer (Mann-Whitney U for winter 2006 and summer 2006/2007: U=276.000; *n*=68, p=0.011; Mann-Whitney U for winter 2007 and summer 2006/2007: U=26.000; *n*=44, p=0.011). Four nematode taxa were found in summer but not in the winter seasons: *Trichostrongylus* sp., *Physaloptera* sp., hookworm type and unidentified spirurid. *Ascaris* sp. was found in winter 2006 and summer 2006/2007, but not in winter 2007. Protozoan PSR was also higher in this troop in summer than winter. The difference between summer and winter 2006 was significant (Mann-Whitney: U=166.000; *n*=68, p<0.001; Figure 4.6.G-H), while the difference between summer and winter 2007 was not. Due to the lack of significant variation between winter seasons (Mann-Whitney U for helminths: U=26.000; *n*=22, p=0.434; for protozoa: U=27.000; *n*=22, p=0.484), data of these two collection periods were pooled for subsequent analyses to increase the magnitude of the sample size.

In summary, there was only one troop for which individuals had significantly different helminth PSR between the same (i.e., winter) seasons, namely Plateau Road. Seasonal differences in helminth PSR were evident for both Da Gama Park and Tokai. However, the pattern of difference was not the same for both troops, with helminth diversity being significantly lower in summer in Da Gama Park and significantly higher in Tokai. Protozoan diversity was significantly higher in summer in one troop, namely the Tokai troop.

4.3.2 Prevalence

Seasonal prevalences of each parasite taxon for each of the four troops are shown in Figure 4.7.A-D. Similar to the PSR results, there was no seasonal variation in parasite prevalence for the individuals in the Buffels Bay troop (Figure 4.7.A). In Da Gama Park, there were significant seasonal differences in the prevalence of six parasite species (Figure 4.7.B), and in all cases there was a higher prevalence in winter compared to summer. The only exception was the protozoan *Chilomastix mesnili*, which was more prevalent in summer (Fisher's Exact test: p=0.042). In the Plateau Road troop, *Trichuris* sp. and *Entamoeba coli* prevalences were significantly higher in winter 2006 than in winter 2007. The only significant difference between seasons was found in *Trichostrongylus* sp., which was more prevalent in summer than winter (Fisher's Exact test: p=0.043). There was no difference in the prevalence of any protozoan taxa across the three sample periods (Figure 4.7.C). In the Tokai troop, the prevalence of *Trichuris* sp. was significantly higher in summer than in both winter seasons (Figure 4.7.D). The same pattern was evident for the protozoa *Entamoeba chattoni*, *E. hartmanni*, and *Iodamoeba bütschlii*, which all had significantly higher prevalence in summer than in winter 2006. The absence of significant differences in the prevalences between the two winter seasons of 2006 and 2007 meant that these data could be pooled to increase the winter sample size for other analyses.

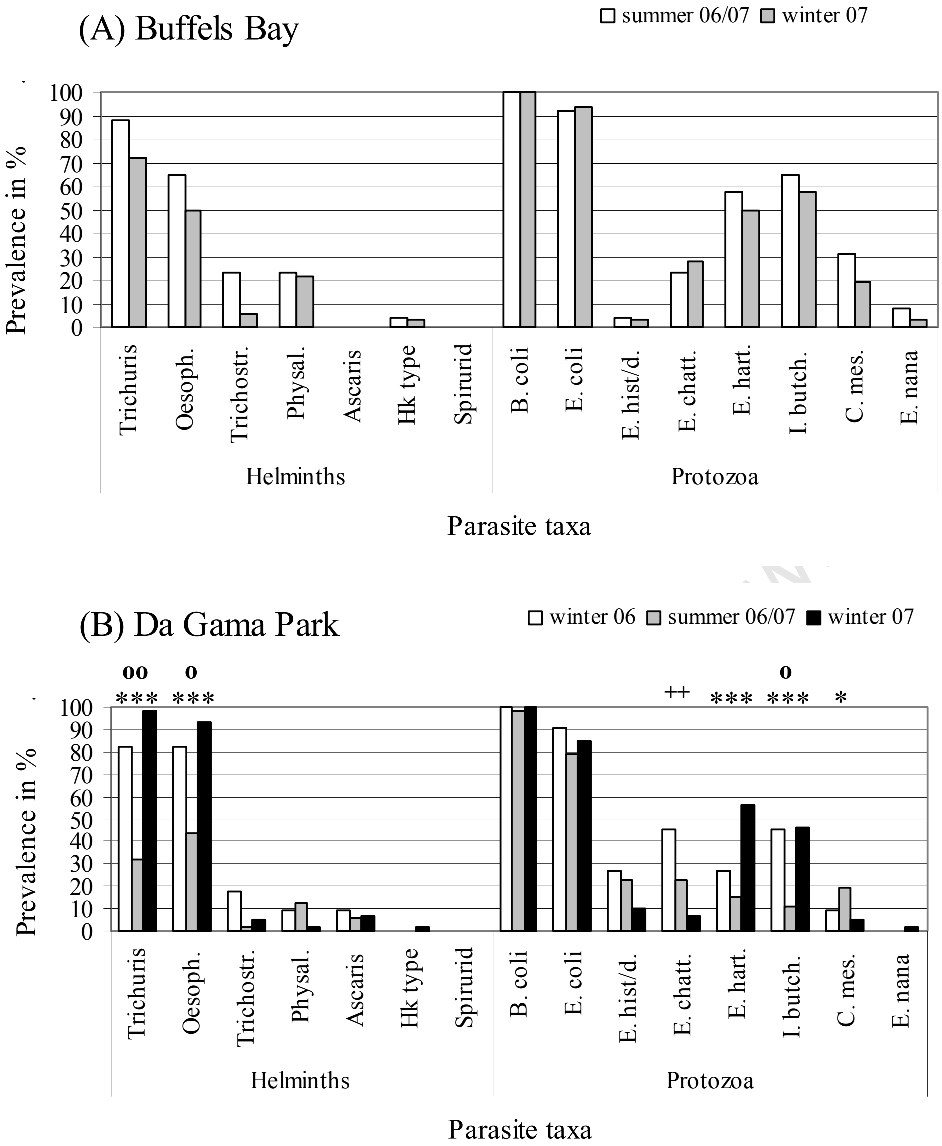
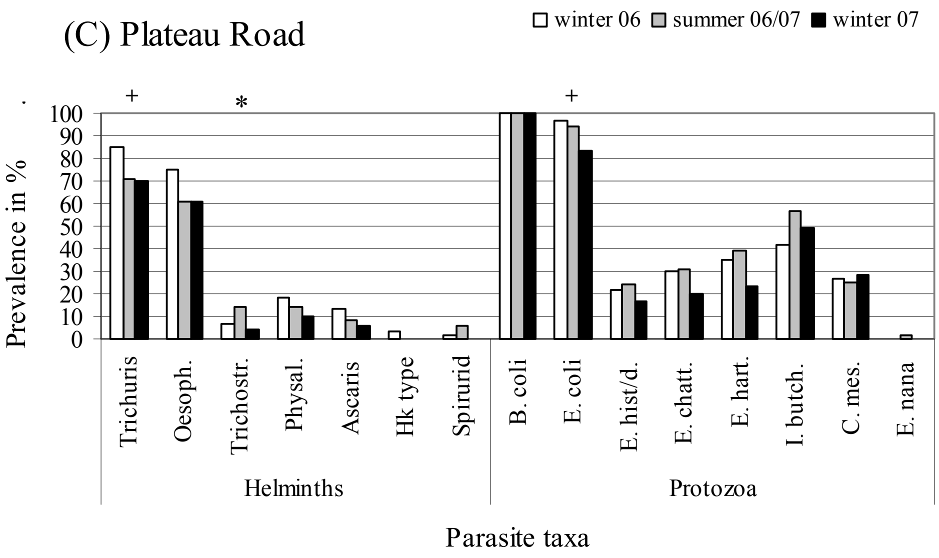


Figure 4.7 Parasite prevalence in winter and summer across two years for individuals in four baboon troops within the Cape Peninsula. Asterisks indicate statistical differences. Fisher's Exact tests: * represent comparison summer 0607 / winter 07; ^{o} represent comparison summer 0607 / winter 06; $^{+}$ represent comparison winter 06 / winter 07. For all tests: *$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$. (Trichuris=*Trichuris* sp., Oesoph.=*Oesophagostomum* sp., Trichostr.=*Trichostrongylus* sp., Physal.=*Physaloptera* sp., Ascaris=*Ascaris* sp., Hk=hookworm, B. coli=*Balantidium coli*, E. coli=*Entamoeba coli*, E. hist/d.=*E. histolytica/dispar*, E. chatt.=*E. chattoni*, E. hart.= *E. hartmanni*, I. butch.=*Iodamoeba butschlii*, C. mesn.=*Chilomastix mesnili*; E. nana=*Endolimax nana*).


(C) Plateau Road

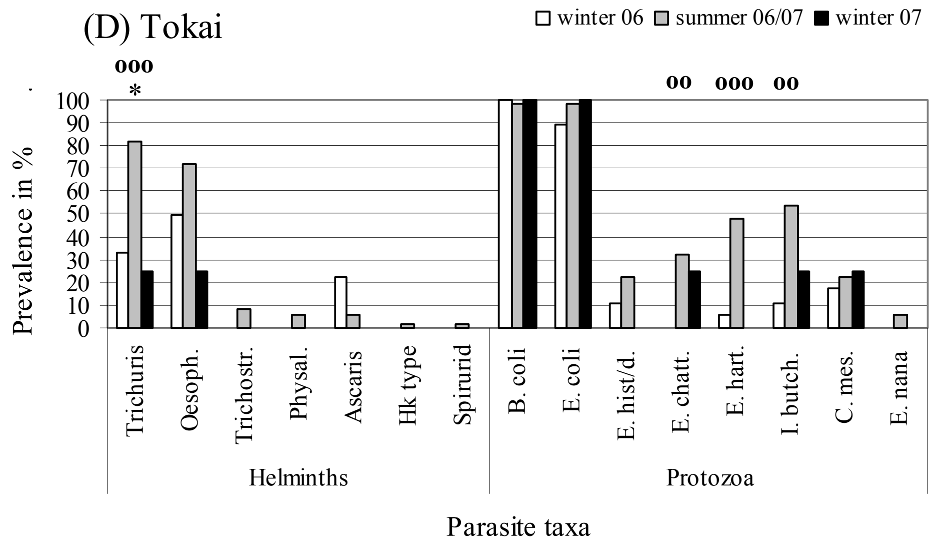
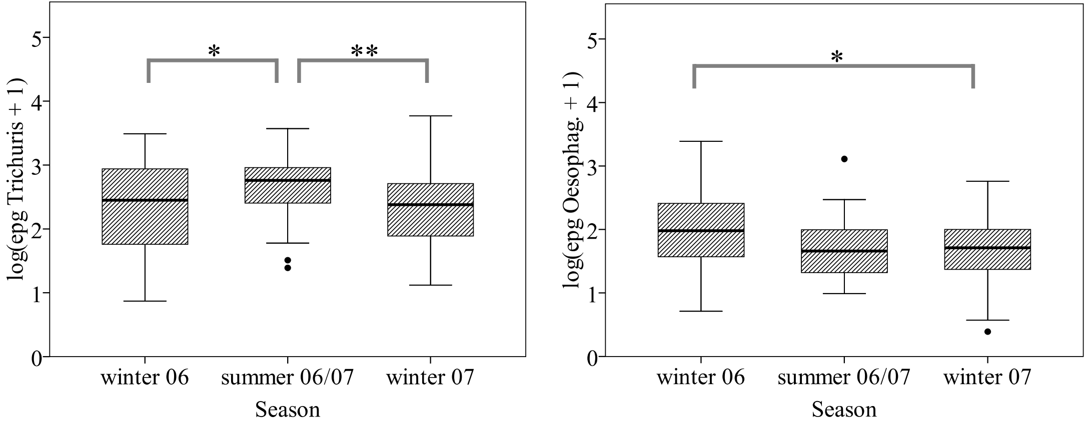

(D) Tokai

Figure 4.7 continued

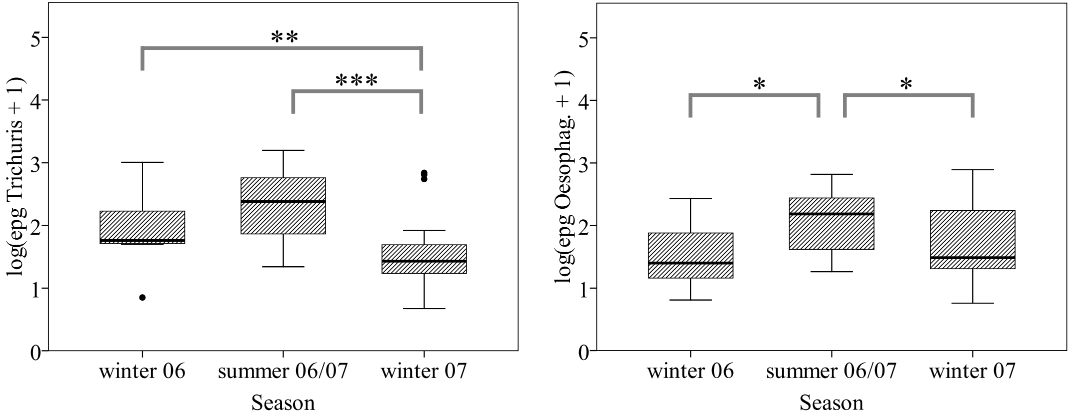
4.3.3 Egg output

This analysis was restricted to the two troops (i.e., Plateau Road and Da Gama Park) for which there were sufficient data. The Kruskal-Wallis tests revealed a significant seasonal variation in *Trichuris* sp. egg output in individuals of the Plateau Road troop (Kruskal-Wallis H: Chi-square=7.860; *n*=142, df=2, p=0.020). Post-hoc Mann-Whitney tests showed that *Trichuris* sp. egg output was significantly higher in summer than in either winter season (Mann-Whitney U tests for winter 2006 and summer 2006/2007: U=680.000; *n*=85, p=0.040;

Mann-Whitney U for summer 2006/2007 and winter 2007: U=656.500; *n*=93, p=0.004; see Figure 4.8.A). Egg output of *Oesophagostomum* sp. did not present any significant seasonal variation (Kruskal-Wallis H: Chi-square=5.267; *n*=123, df=2, p=0.072; Figure 4.8.B). In the Da Gama Park troop, *Trichuris* sp. egg output varied significantly between seasons (Kruskal-Wallis H: Chi-square=23.082; *n*=69, df=2, p<0.001). Post-hoc tests showed a significantly higher egg output in summer 2006/2007 than in winter 2007 (Mann-Whitney U: U=111.000; *n*=60, p<0.001), and a significantly higher egg output in winter 2006 than in winter 2007 (Mann-Whitney U: U=82.500; *n*=49, p=0.010) (Figure 4.8.C).


(A) Plateau Road, Trichuris sp.

(B) Plateau Road, Oesophagostomum sp.


(C) Da Gama Park, Trichuris sp.

(D) Da Gama Park, Oesophagostomum sp.

Figure 4.8.(A-D) Mean egg output of *Trichuris* sp. and *Oesophagostomum* sp. for individuals in the Plateau Road and Da Gama Park troops across three seasonal periods. The boxes show interquartile ranges, the bold horizontal bars give the median. The end of the 'whiskers' represent the largest and smallest values that are not outliers or extreme values. The circles represent outliers. Asterisks indicate statistical differences: Mann-Whitney U test: *p≤ 0.05, **p≤ 0.01, ***p≤ 0.001.

Oesophagostomum sp. egg production also presented seasonal variations (Kruskal-Wallis H: Chi-square=8.016; *n*=73, df=2, p=0.018), showing significantly higher values in summer than in either winter season (Mann-Whitney U for winter 2006 and summer 2006/2007: U=53.000; *n*=35, p=0.015; Mann-Whitney U for summer 2006/2007 and winter 2007: U=325.500; *n*=64, p=0.021; Figure 4.8.D).

4.4 Parasite infections in the Cape Peninsula baboons

4.4.1 Parasite species richness

The average number of taxa per sample across the six Cape Peninsula troops investigated was two helminths and three protozoa. The medians showed the same values (Figure 4.9).

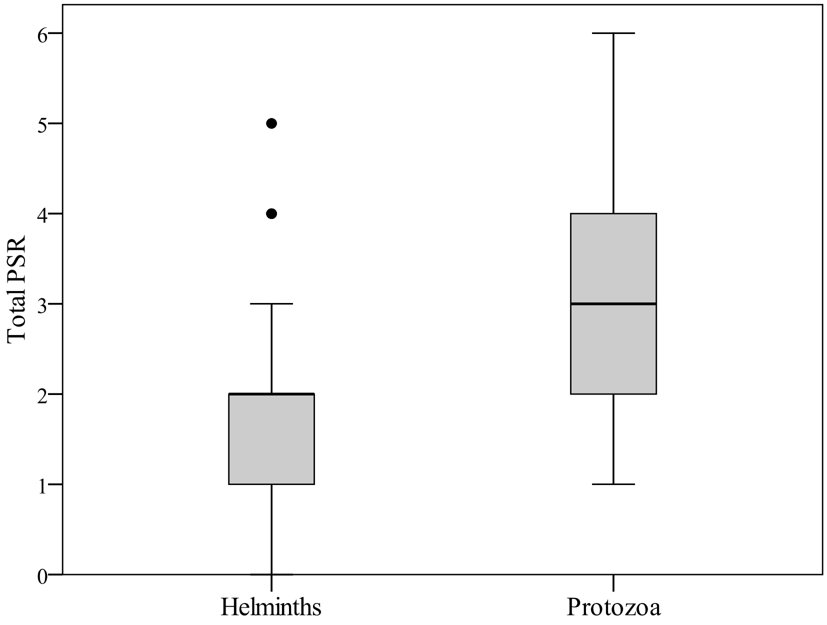


Figure 4.9 Parasite species richness for the Cape Peninsula population. The boxes show the interquartile ranges, bold horizontal bars show the median. The ends of the 'whiskers' represent the minimum and maximum values that are not outliers. The circles represent outliers.

4.4.2 Prevalence

The prevalence estimate for the Cape Peninsula baboon population was calculated from the average of the six study troops (Figure 4.10). The highest helminth prevalence was for *Trichuris* sp. (66%) followed by *Oesophagostomum* sp. (61%). The highest protozoan prevalence was *Balantidium coli* (100%) with *Entamoeba coli* (91%) second. The prevalence of helminths other than *Trichuris* sp. and *Oesophagostomum* sp. were all below 10%.

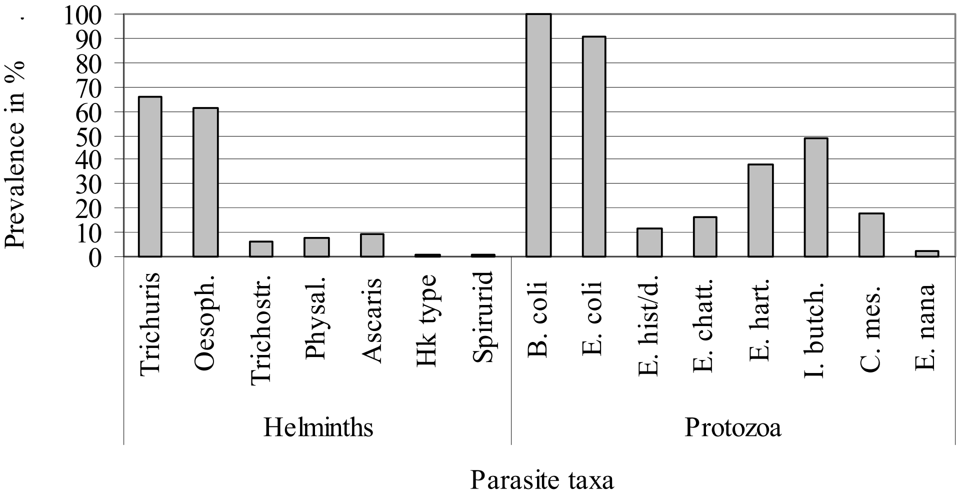


Figure 4.10 The percentage prevalence for all parasite taxa identified in the Cape Peninsula baboon population. (Trichuris=*Trichuris* sp., Oesoph.=*Oesophagostomum* sp., Trichostr.=*Trichostrongylus* sp., Physal.=*Physaloptera* sp., Ascaris=*Ascaris* sp., Hk=hookworm, B. coli=*Balantidium coli*, E. coli=*Entamoeba coli*, E. hist/d.=*E. histolytica/dispar*, E. chatt.=*E. chattoni*, E. hart.= *E. hartmanni*, I. butch.=*Iodamoeba butschlii*, C. mesn.=*Chilomastix mesnili*; E. nana=*Endolimax nana*).

4.4.3 Multiple infections

The frequency of multiple-species infections (i.e., the proportion of samples with >1 parasite species) in the Cape Peninsula was high for both helminths (60.9%) and protozoa (93.0%) (Figure 4.11). The mode for frequency distribution of helminth and protozoan taxa was two and three respectively. For the rest, it is possible to see that the highest proportion of samples was infected with two helminths (45.4%), *Trichuris* sp. and *Oesophagostomum* sp. in most of the cases (87.0%), and three protozoa (28.8%).

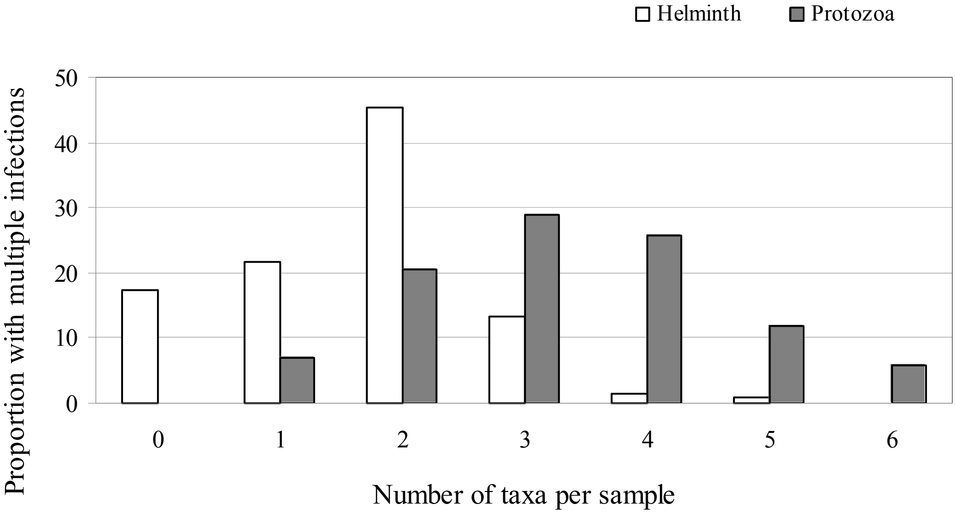


Figure 4.11 The frequency distribution of the proportion of samples that were infected by parasites of either helminth or protozoan parasite taxa.

4.4.4 Egg output

Egg output was found to vary significantly according to the parasite species (Kruskal-Wallis H: Chi-Square=60.973; *n*=311, df=4, p<0.001). *Trichuris* sp. had the highest egg output with a median of 74.3 eggs emitted per gram of faeces, followed by *Oesophagostomum* sp. (32.3 eggs per gram of faeces), and *Physaloptera* sp. (20.7 eggs per gram of faeces) (Table 4.3).

Table 4.3 Faecal egg output (refers to number of eggs per gram of faecal sediment). *n* gives the number of faecal samples that were positive for a specific parasite. SD is the standard deviation, Min the minimum and Max the maximum.

Parasite taxa	*n*	Mean	Median	SD	Min	Max	Range
Trichuris sp.	143	310.0	74.3	752.4	4	5911	5907
Oesophagostomum sp.	129	104.0	32.3	163.5	1	783	782
Trichostrongylus sp.	9	6.0	4.3	6.4	1	19	18
Physaloptera sp.	18	35.0	20.7	39.0	2	114	112
Ascaris sp.	12	10.0	7.9	7.6	1	22	21

4.5 Comparison with baboon parasites across Africa

Helminth species diversity in the Cape Peninsula included seven taxa. The highest helminth diversity in southern Africa was found in Mkuzi Game Reserve (Appleton *et al.* 1991) and unknown localities in Zimbabwe (Goldsmid 1974), with 12 and 10 helminth taxa, respectively. The lowest helminth diversity was found in Namibia, with only three taxa (Appleton & Brain 1995). The helminths most frequently reported were *Physaloptera* sp., found in all localities except Namibia, and *Oesophagostomum* sp., *Trichostrongylus* sp., and *Streptopharagus* sp., found in 12 of the 14 baboon studies. *Streptopharagus* was not found in the Cape Peninsula population. *Trichuris* was also a species common to most other study sites across South Africa being present in 10 out 14 sites. Remarkably, the nematode *Ascaris* sp. was found only in the Cape Peninsula. Another common helminth was the cestode *Bertiella studeri*, which was found in 70% of all studies but was not observed in any of the Cape Peninsula samples.

Eight protozoan taxa were found in the Cape Peninsula, including two parasites and six commensals. *Balantidium coli*, *Entamoeba coli*, and *Iodamoeba butschlii* were the most common protozoa, found in every locality where protozoan fauna was reported. The other protozoa taxa reported in this study were also commonly found in the other sites.

Prevalences varied significantly among sites (Table 4.4). Prevalences of helminths in the Cape Peninsula were most similar to prevalences in the former Northern Transvaal's baboons. Prevalence of *Trichuris* sp. was lower in baboons in the Cape Peninsula than in Pringle Bay and Wildcliff, but was higher than in any other population analyzed in South Africa (Appendix E). Apart from Giant's Castle, this nematode presented low prevalences in the rest of study sites. *Oesophagostomum* sp. was found in almost every population studied and its prevalence was higher in five other locations than it was in the Cape Peninsula population. Prevalences of *Trichostrongylus* sp. and *Physaloptera* sp. in Cape Peninsula were lower than in the majority of the other baboon populations studied. Prevalences of protozoa were most similar between the Cape Peninsula and the neighbouring population Pringle Bay and, to a lesser extent, Wildcliff and the former Northern Transvaal. Prevalences of *Balantidium coli* and *Entamoeba coli* were in general high in every baboon population, and were particularly high in the Cape Peninsula population. Prevalence of *E. histolytica* in the Cape Peninsula population was higher than in other study areas. However, it must be remembered that identification of this parasite included the morphologically identical commensal protozoan *E. dispar*. Other protozoan taxa (*E. chattoni*, *E. hartmanni*, *I. bütschlii*, *E. nana*, and *C. mesnili*), all of which are non-pathogenic, had low prevalences in all of the South African study populations.

Table 4.4 Prevalence (%) of gastrointestinal parasites found in chacma baboon (*Papio ursinus*) at different localities across South Africa.

	Locations												
	Cape Peninsula (present study)	Pringle Bay (present study)	Wildcliff Nature Reserve (present study)	Giant's Castle Game Reserve (Appleton *et al.* 1986)	Mkuzi Game Reserve (Appleton *et al.* 1991)	Suikerbosrand Nature Reserve (Pettifer 1984)	Loskop Dam Nature Reserve (Pettifer 1984)	Scrutton Private Nature Reserve (Pettifer 1984)	Northern Transvaal (Goldsmid & Rogers 1978)	South Africa (Myers *et al.* 1971)	CHI-SQ	df	p
Nematoda													
Trichuris sp.	66	89	98	57	6	0	2	0	4	22	373.696	9	**<0.001**
Oesophagostomum sp.	61	91	38	49	15	100	95	100	63	0	284.433	9	**<0.001**
Trichostrongylus sp.	6	100	48	0	1	92	30	44	8	11	430.281	9	**<0.001**
Physaloptera sp.	8	54	78	44	2	10	97	78	4	12	414.190	9	**<0.001**
Protozoa													
Balantidium coli	100	77	66	26	80				54	46	277.120	6	**<0.001**
Entamoeba coli	91	94	92	70	75				54	37	107.078	6	**<0.001**
Entamoeba histolytica	12	6	2	0	0				0	3	47.507	6	**<0.001**
Entamoeba chattoni	16	6	28	0	0				0	15	73.891	6	**<0.001**
Entamoeba hartmanni	38	17	16	0	0				0	11	159.000	6	**<0.001**
Iodamoeba butschlii	49	40	72	2	9				4	22	191.075	6	**<0.001**
Endolimax nana	2	0	0	10	13				0	11	35.377	6	**<0.001**
Chilomastix mesnili	18	29	10	13	0				4	0	57.655	6	**<0.001**

CHAPTER FIVE

HOST-INDIVIDUAL FACTORS

5.1 Intra-individual variation

Species of helminths found in two consecutive samples from the same individual on the same day corresponded in half of the four cases analyzed. In one case, *Oesophagostomum* sp. was found in the first sample but not in the second. This result is not unusual, since the numbers of eggs produced by nematodes are known to vary considerably (Anderson & Schad 1985; Gillespie 2006). In the other case, *Trichuris* sp. was present in the first sample collected but not in the second. Due to the high number of *Trichuris* sp. eggs found per sample, it is more difficult to understand why one sample would contain many more eggs than another would. Variation between consecutive samples from the same host was also noted in protozoa. In two cases, *Entamoeba histolytica/dispar* and *E. hartmanni* were found in only one of the two samples collected for a known baboon. Two different baboons excreted cysts of *E. chattoni* and *Iodamoeba bütschlii* in one scat but not in the other.

The analysis of intra-individual variation over the entire study period revealed that only 29% of individuals analyzed had eggs of *Trichuris* sp. in all repeat samples. Results for the other helminth taxa were even less uniform, with examples of the stages of *Oesophagostomum* sp. being present in only 18% of individuals in all the repeat samples. Eggs of *Trichostrongylus* sp., *Physaloptera* sp., and *Ascaris* sp. were sampled from 14, 17, and 10 baboons respectively, and their presence in repeat samples also never reached 100%.

Intra-individual temporal variation was also high amongst the protozoan species, with the exception of *Balantidium coli*. In the latter species, almost all samples for all individuals (96%) were positive. In conclusion, egg and cyst output varied between samples collected from the same individual, supporting the prediction of temporal variation.

5.2 Age and sex

5.2.1 Parasite species richness

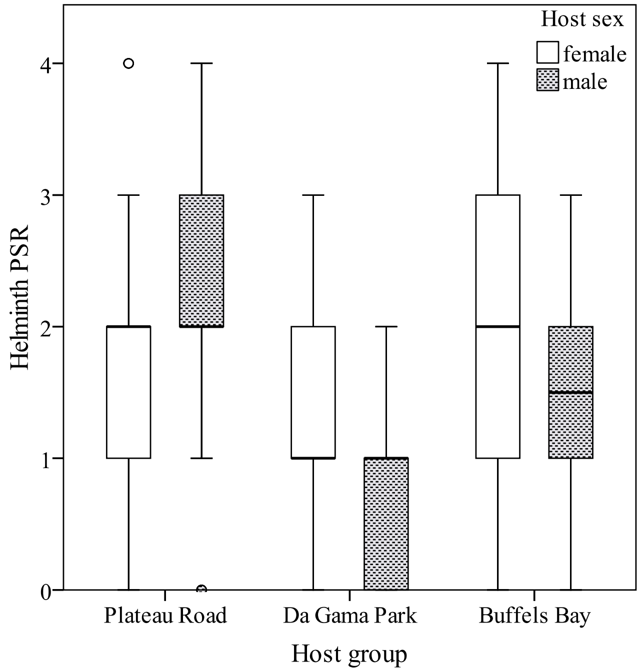
Helminth PSR did not show significant sex-specific variability in any of the three troops investigated (Figure 5.1.A; Mann-Whitney test: Plateau Road U=1993.0, n_{female}=106, n_{male}=41, p=0.410; Da Gama Park U=363.0, n_{female}=35, n_{male}=27, p=0.096; Buffels Bay: U=199.0, n_{female}=40, n_{male}=12, p=0.356). Similarly there was no difference in the PSR of protozoa in males and females in all three troops (Figure 5.1.B; Mann-Whitney test: Plateau Road U=2061.0, n_{female}=106, n_{male}=41, p=0.619; Da Gama Park U=435.5, n_{female}=35, n_{male}=27, p=0.569; Buffels Bay: U=234.5, n_{female}=40, n_{male}=12, p=0.898).

Helminth PSR was higher in adults than juveniles for all three troops analyzed (Figure 5.2.A; Mann-Whitney test: Plateau Road U=1795.0, n_{juvenile}=53, n_{adult}=86, p=0.027; Da Gama Park U=96.0, n_{juvenile}=19, n_{adult}=39, p<0.001; Tokai: U=65.5, n_{juvenile}=16, n_{adult}=45, p<0.001). Protozoan PSR was only significantly higher in adults compared to juveniles in the Tokai troop (Figure 5.2.B; Mann-Whitney test: Tokai U=187.5, n_{juvenile}=16, n_{adult}=45, p=0.004). There was no significant difference between adults and juveniles in either of the other two troops (Mann-Whitney test: Plateau Road U=2088.0, n_{juvenile}=53, n_{adult}=86, p=0.396; Da Gama Park U=277.0, n_{juvenile}=19, n_{adult}=39, p=0.097).

5.2.2 Prevalence

Apart from the protozoan *E. histolytica/dispar*, the prevalence of helminth and protozoan species did not differ significantly between males and females in all three troops (Figure 5.3.A, B, and C). *E. histolytica/dispar* was however more prevalent in females than males in the Plateau Road troop (Fisher's Exact p=0.043; see asterisk in Figure 5.3.A).

(A) Helminths



(B) Protozoa

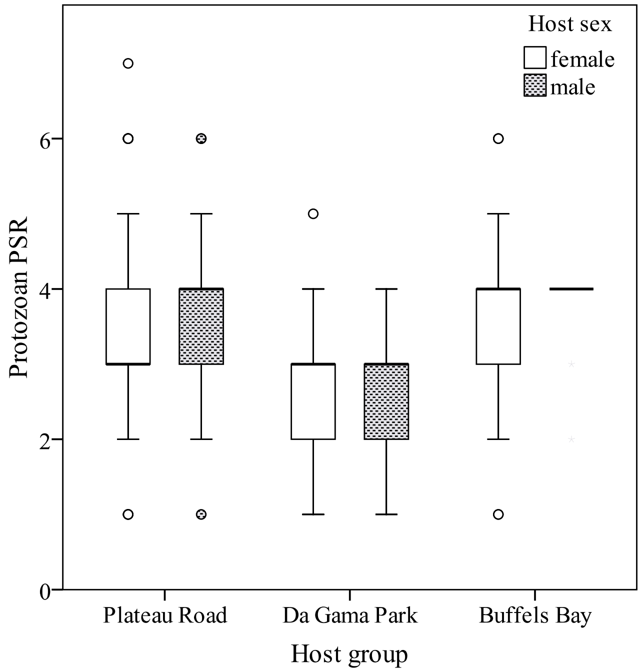
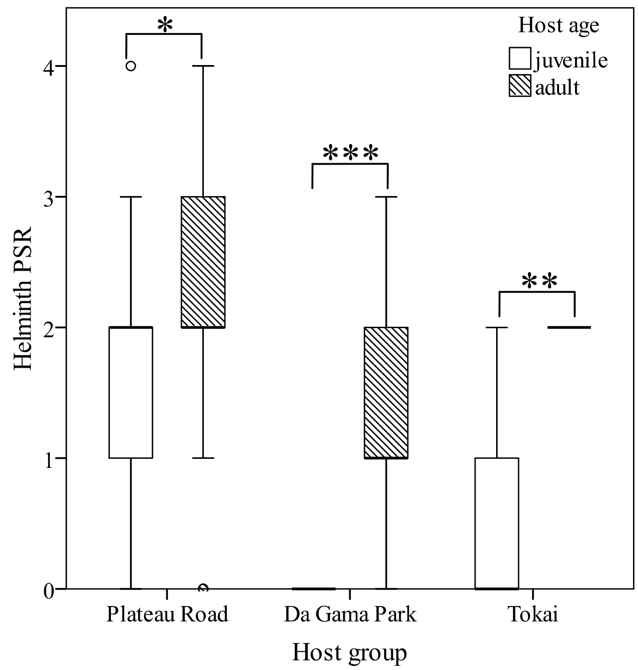


Figure 5.1.(A-B) Helminth (A) and protozoan (B) species richness in females versus males in three Cape Peninsula troops. The boxes show the interquartile ranges, bold horizontal bars show the median. The ends of the whiskers represent the minimum and maximum values that are not outliers. The circles represent outliers.

(A) Helminths



(B) Protozoa

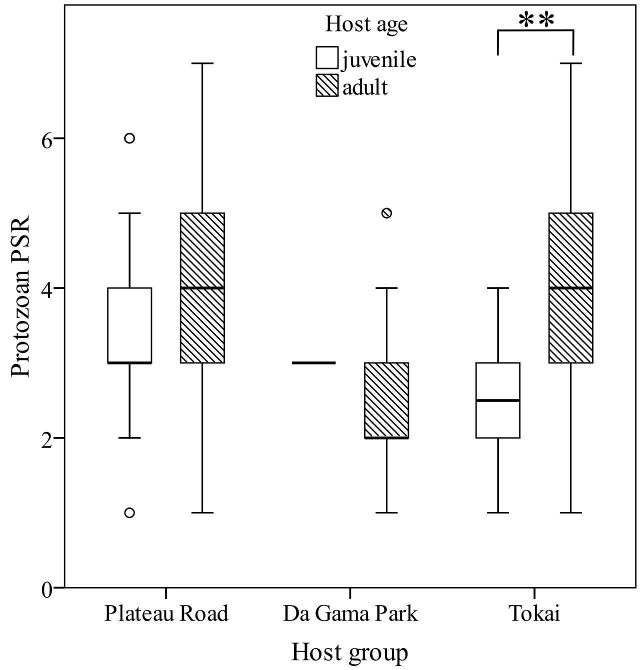


Figure 5.2.(A-B) Helminth (A) and protozoan (B) species richness in adults versus juveniles in three Cape Peninsula troops. The boxes show the interquartile ranges, bold horizontal bars show the median. The ends of the whiskers represent the minimum and maximum values that are not outliers. The circles represent outliers. Asterisks indicate statistical differences between ages: Mann-Whitney U test: *$p \leq 0.05$; **$p \leq 0.01$; ***$p \leq 0.001$.

The prevalence of *Trichuris* sp. was significantly higher in adults than in juveniles in all three troops (Figure 5.4.A, B, and C; Fisher's Exact test: Plateau Road p=0.004; Da Gama Park p=0.016; Tokai p<0.001). Similar results were obtained for another nematode, *Oesophagostomum* sp., with adults having higher prevalence in both the Da Gama Park (Fisher's Exact test: p<0.001) and Tokai troops (Fisher's Exact test: p=0.002). Significant differences were also evident in the prevalence of protozoan taxa between adults and juveniles (Figure 5.4.A, B, and C) including: *E. histolytica/dispar* (Fisher's Exact test: Plateau Road p=0.002; Tokai p=0.014); *E. chattoni* (Fisher's Exact test: Tokai p=0.014); *I. butschlii* (Fisher's Exact test: Tokai p=0.043). In all these cases the prevalence was higher in adults than juveniles with the only exception being the protozoan *E. coli*, which in the Da Gama Park troop was significantly higher in juveniles (Fisher's Exact p=0.043).

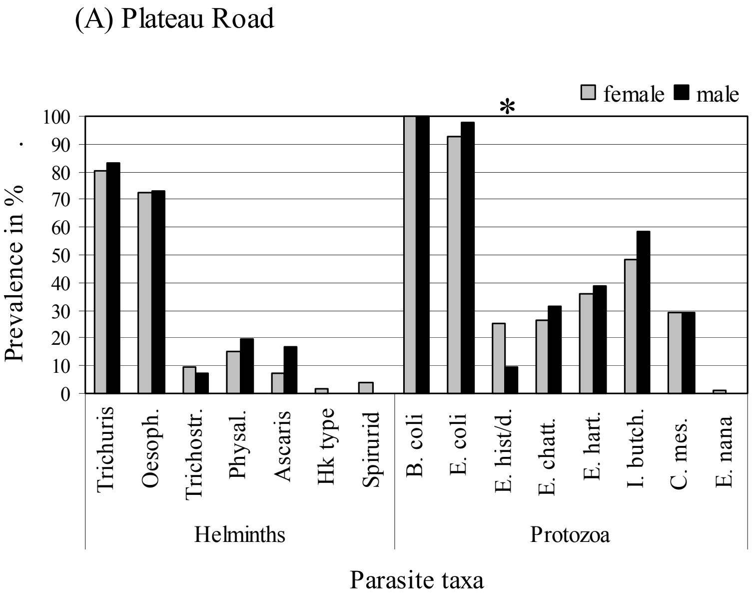
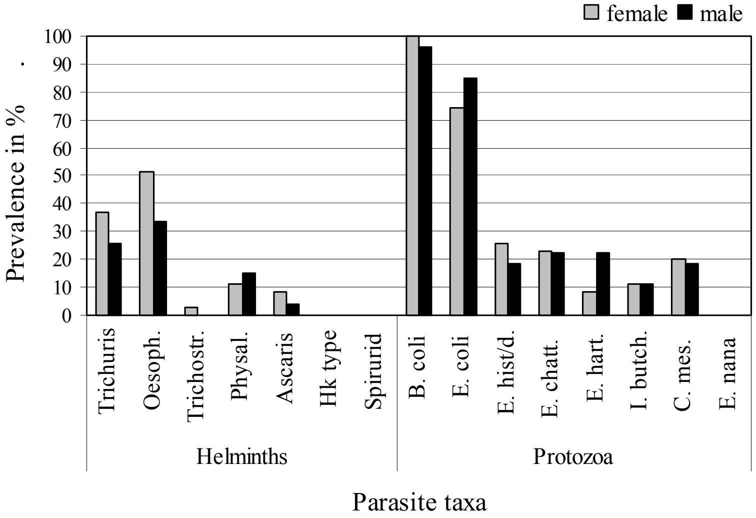


Figure 5.3.(A-C) Parasite prevalences in female and male baboons in three troops in the Cape Peninsula. Bars denote prevalence per parasite species for samples obtained from females and males within each troop. Asterisks indicate statistical differences: Pearson Chi-square: * p≤ 0.05. (Trichuris=*Trichuris* sp., Oesoph.=*Oesophagostomum* sp., Trichostr.=*Trichostrongylus* sp., Physal.=*Physaloptera* sp., Ascaris=*Ascaris* sp., Hk =hookworm, B. coli=*Balantidium coli*, E. coli=*Entamoeba coli*, E. hist/d.=*E. histolytica/dispar*, E. chatt.=*E. chattoni*, E. hart.= *E. hartmanni*, I. butch.=*Iodamoeba butschlii*, C. mesn.=*Chilomastix mesnili*; E. nana=*Endolimax nana*).

(B) Da Gama Park



(C) Buffels Bay

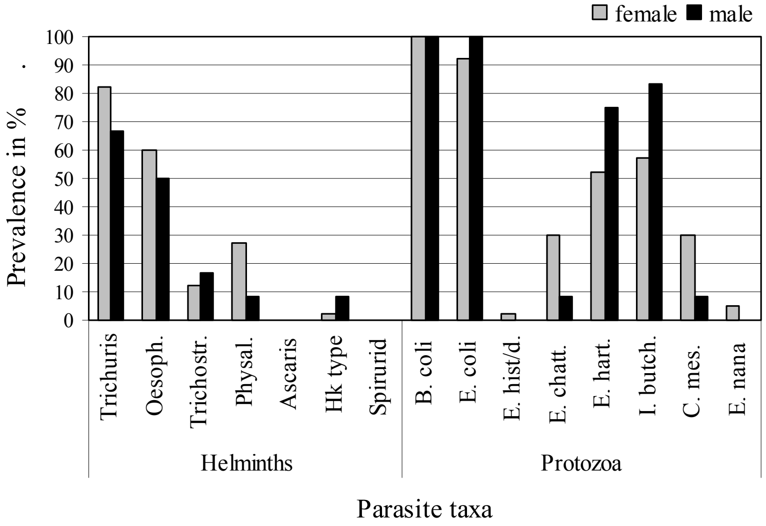
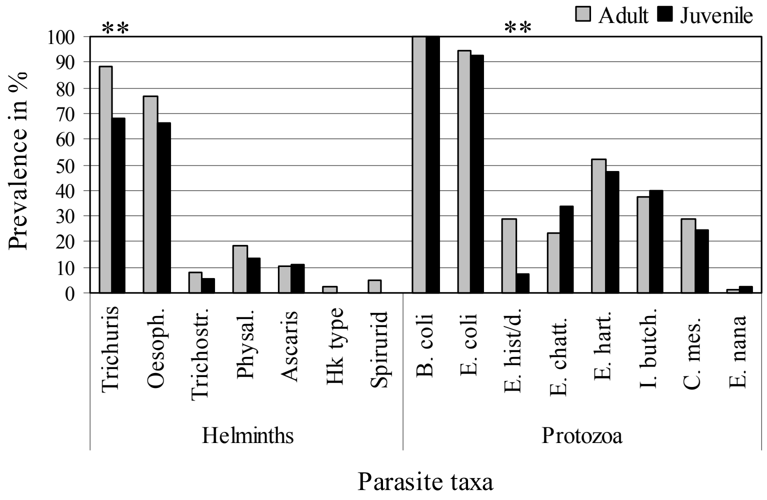


Figure 5.3.(A-C) continued

(A) Plateau Road



(B) Da Gama Park

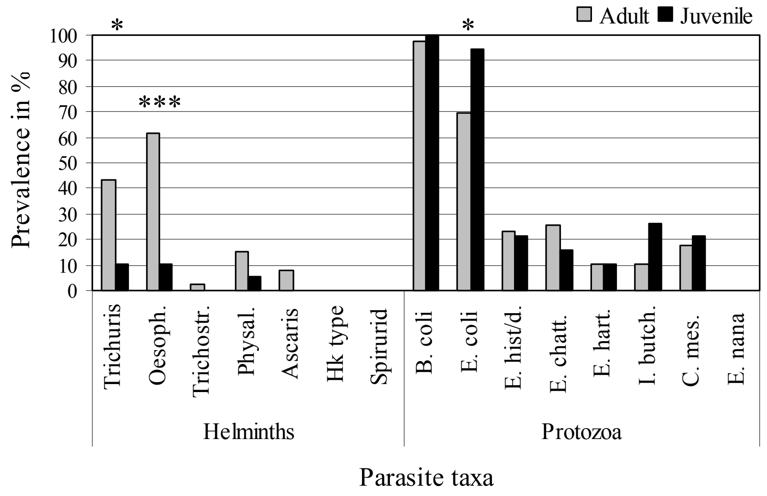


Figure 5.4.(A-C) Parasite prevalences in adult and juvenile baboons in three troops in the Cape Peninsula. Bars denote prevalence per parasite species for samples from adults and juveniles. Asterisks indicate statistical differences: Pearson Chi-square: * p≤ 0.05; **p≤ 0.01; ***p≤ 0.001. (Trichuris=*Trichuris* sp., Oesoph.=*Oesophagostomum* sp., Trichostr.=*Trichostrongylus* sp., Physal.=*Physaloptera* sp., Ascaris=*Ascaris* sp., Hk =hookworm, B. coli=*Balantidium coli*, E. coli=*Entamoeba coli*, E. hist/d.=*E. histolytica/dispar*, E. chatt.=*E. chattoni*, E. hart.= *E. hartmanni*, I. butch.=*Iodamoeba butschlii*, C. mesn.=*Chilomastix mesnili*; E. nana=*Endolimax nana*).

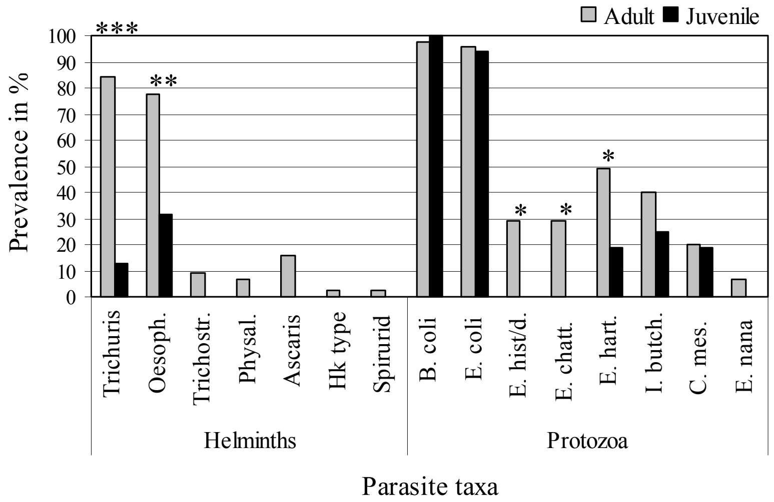

(C) Tokai

Figure 5.4.(A-C) continued

5.3 Reproductive status

There was no difference in the helminth species richness of cycling, pregnant, and lactating female baboons; they were all infected with an average of two nematode taxa. Cycling and lactating females harboured on average three different types of protozoa, while pregnant females had a total of four protozoan taxa. Similarly, there was no significant difference in the prevalence of helminths or protozoa among females of different reproductive status (Figure 5.5). The only exception was *Entamoeba hartmanni*, which was significantly more prevalent in lactating females than pregnant females (Fisher's Exact p=0.007; see asterisk in Figure 5.5).

There was no difference in egg production of both *Trichuris* sp. and *Oesophagostomum* sp. between females of different reproductive status (Kruskal-Wallis test; *Trichuris* sp.: H=4.598, *n*=125, p=0.100; *Oesophagostomum* sp.: H=4.973, *n*=116, p=0.083). Similar results were obtained for the protozoan taxa *Balantidium coli* (Kruskal-Wallis H=1.184, *n*=153, p=0.553), *Entamoeba coli* (Kruskal-Wallis H=0.750, *n*=137, p=0.687), *E. histolytica/dispar* (Kruskal-Wallis H=2.837, *n*=41, p=0.242), and *E. chattoni* (Kruskal-Wallis H=3.176, *n*=39, p=0.204) when compared between females of different reproductive status.

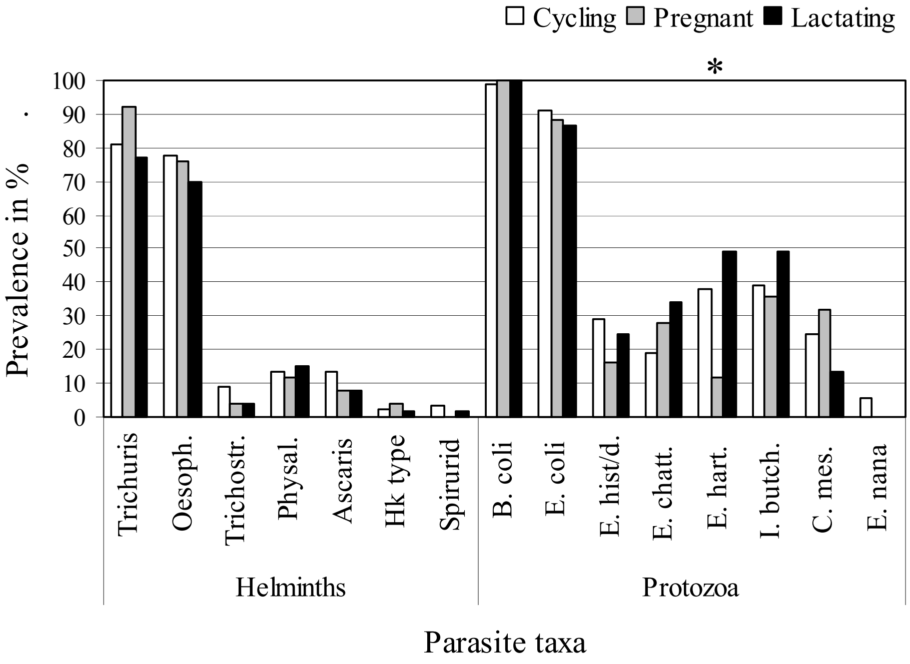


Figure 5.5 Parasite prevalences for cycling, pregnant, and lactating baboon females in three troops in the Cape Peninsula. Bars denote prevalence per parasite species for samples from cycling, pregnant, and lactating female states. Asterisks indicate statistical differences: Pearson Chi-square: * p≤ 0.05, ** p≤ 0.01. (Trichuris=*Trichuris* sp., Oesoph.=*Oesophagostomum* sp., Trichostr.=*Trichostrongylus* sp., Physal.=*Physaloptera* sp., Ascaris=*Ascaris* sp., Hk =hookworm, B. coli=*Balantidium coli*, E. coli=*Entamoeba coli*, E. hist/d.=*E. histolytica/dispar*, E. chatt.=*E. chattoni*, E. hart.= *E. hartmanni*, I. butch.=*Iodamoeba butschlii*, C. mesn.=*Chilomastix mesnili*; E. nana=*Endolimax nana*).

5.4 Social status

Helminth and protozoan species diversity did not vary significantly between female baboons of high, medium, and low social status (Helminths: Kruskal-Wallis H=2.256, *n*=18, p=0.324; Protozoa: Kruskal-Wallis H=1.861, *n*=18, p=0.394). The prevalences of helminths and protozoa were not significantly different between high, medium, and low ranking females, with the exception of the nematode *Trichostrongylus* sp. (Fisher's Exact p=0.005; see asterisk in Figure 5.6), which was significantly higher in high ranking than low ranking females. This particular parasite was not found in any medium ranking females.

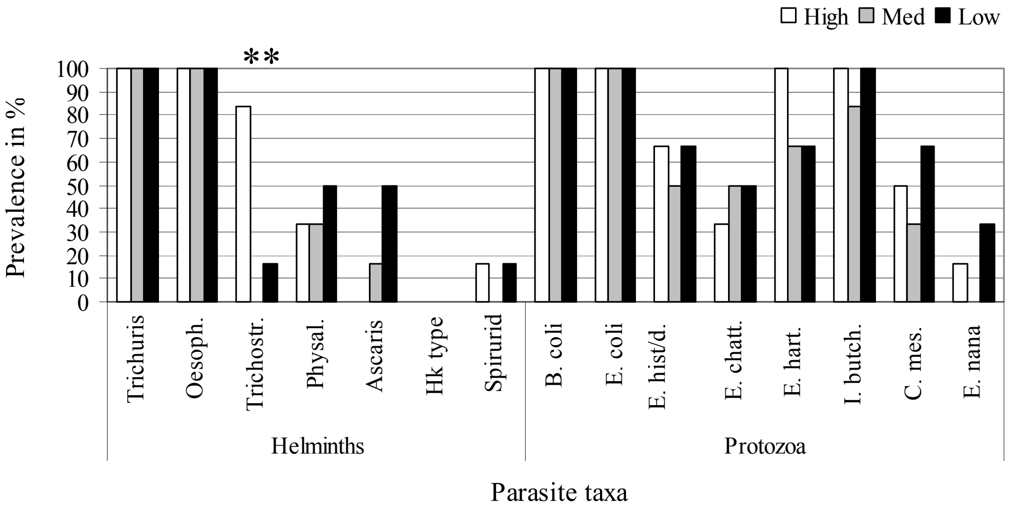


Figure 5.6 Parasite prevalences for high, medium, and low ranking baboon females in three troops in the Cape Peninsula. Bars denote prevalence per parasite species for samples from high, medium, and low female ranking states. Asterisks indicate statistical differences: Pearson Chi-square: * p≤ 0.05, ** p≤ 0.01. (Trichuris=*Trichuris* sp., Oesoph.=*Oesophagostomum* sp., Trichostr.=*Trichostrongylus* sp., Physal.=*Physaloptera* sp., Ascaris=*Ascaris* sp., Hk =hookworm, B. coli=*Balantidium coli*, E. coli=*Entamoeba coli*, E. hist/d.=*E. histolytica/dispar*, E. chatt.=*E. chattoni*, E. hart.= *E. hartmanni*, I. butch.=*Iodamoeba butschlii*, C. mesn.=*Chilomastix mesnili*; E. nana=*Endolimax nana*).

There was no significant difference in average egg and cyst production between high, medium, and low ranking female baboons for any of the parasite taxa investigated (*Trichuris* sp.: Kruskal-Wallis H=0.484, *n*=17, p=0.785; *Oesophagostomum* sp.: Kruskal-Wallis H=0.964, *n*=17, p=0.618; *Trichostrongylus* sp.: Mann-Whitney U=3.000, *n*=6, p=0.643; *Physaloptera* sp.: Kruskal-Wallis H=4.418, *n*=10, p=0.110; *Ascaris*: Kruskal-Wallis H=0.238, *n*=6, p=0.888; *Entamoeba coli*: Kruskal-Wallis H=0.410, *n*=17, p=0.815; *E. histolytica/dispar*: Kruskal-Wallis H=1.856, *n*=12, p=0.395; *E. chattoni*: Kruskal-Wallis H=2.333, *n*=10, p=0.311; *E. hartmanni*: Kruskal-Wallis H=1.625, *n*=14, p=0.444; *Iodamoeba bütschlii*: Kruskal-Wallis H=5.115, *n*=16, p=0.078; *Chilomastix mesnili*: Kruskal-Wallis H=0.960, *n*=14, p=0.619).

CHAPTER SIX

GROUP-LEVEL AND HABITAT FACTORS: AN INTER-TROOP ANALYSIS

6.1 Comparison of parasite infection between Cape Peninsula troops

Helminth and protozoan species richness varied significantly between the six troops (Kruskal Wallis H=32.978, df=5, p<0.001 and H=23.105, df=5, p<0.001 for helminths and protozoa, respectively) (Figure 6.1; Figure 6.2). Tokai troop harboured significantly less helminth species than all the other troops, except Cape Point (Mann-Whitney U tests; between Tokai and Buffels Bay: U=270.000; *n*=58, p=0.036; between Tokai and Kanonkop: U=376.000; *n*=90, p<0.001; between Tokai and Plateau Road: U=644.000; *n*=105, p=0.027; between Tokai and Da Gama Park: U=162.500; *n*=63, p<0.001) (Figure 6.1).

Helminth diversity was significantly higher in Da Gama Park than Buffels Bay (Mann-Whitney U test: U=493.000; *n*=77, p=0.006), Cape Point (Mann-Whitney U test: U=164.000; *n*=62, p<0.001), and Plateau Road (Mann-Whitney U test: U=1152.500; *n*=124, p=0.001) troops (Figure 6.1), while helminth diversity was significantly higher in Kanonkop compared to both Plateau Road troop (Mann-Whitney U test: U=2263.500; *n*=151, p=0.026) and Cape Point troop (Mann-Whitney U test: U=382.000; *n*=89, p=0.001) (despite Kanonkop and Plateau Road having similar medians; Figure 6.1).

Protozoan parasite species richness (PSR) had a similar overall trend to helminth PSR, with Tokai troop having significantly fewer helminth taxa compared to the other five troops investigated (Mann-Whitney U tests; between Tokai and Buffels Bay: U=175.500; *n*=58, p<0.001; between Tokai and Cape Point: U=87.000; *n*=43, p<0.001; between Tokai and Kanonkop: U=313.500; *n*=90, p<0.001; between Tokai and Plateau Road: U=596.000; *n*=105, p=0.010; between Tokai and Da Gama Park: U=303.000; *n*=63, p=0.027) (Figure 6.2). These differences were most pronounced between Tokai and the three troops (Buffels Bay, Cape Point, and Kanonkop) that reside within the Cape of Good Hope (CoGH) Section of the Table

Mountain National Park (TMNP). Tokai was the least different from its nearest geographic neighbour, the Da Gama Park troop.

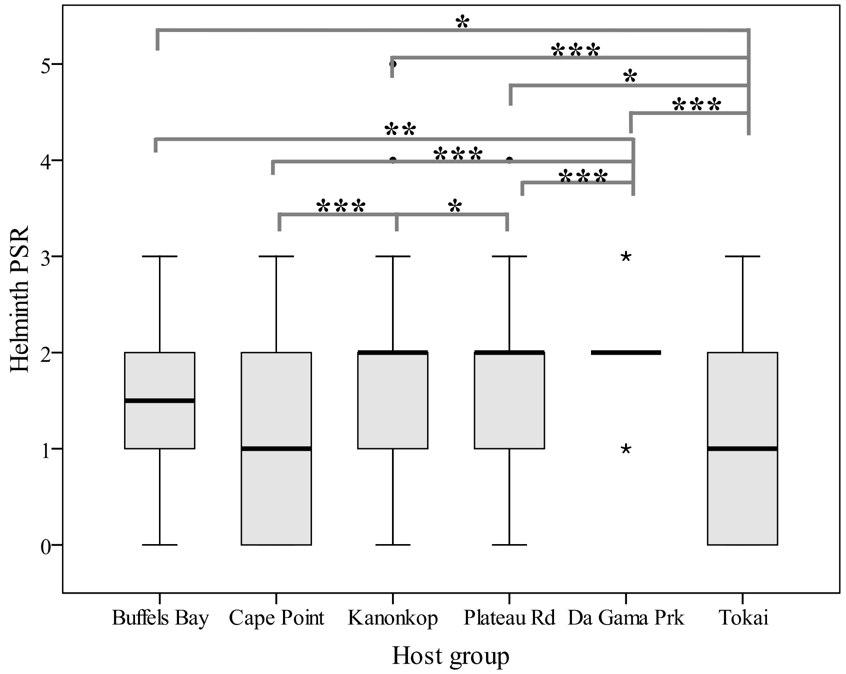


Figure 6.1 Helminth species richness per baboon troop. The boxes show the interquartile ranges, bold horizontal bars show the median. The ends of the 'whiskers' represent the minimum and maximum values that are not outliers. Outliers: circles and stars. Asterisks indicate statistical differences between groups: Mann-Whitney U test: *p≤ 0.05; **p≤ 0.01; ***p≤ 0.001.

Kanonkop protozoan richness was significantly higher than that of the Plateau Road (Mann-Whitney U test: U=2235.000; *n*=151, p=0.024) and Da Gama Park (Mann-Whitney U test: U=1030.000; *n*=109, p=0.019) troops (Figure 6.2). There was no difference in the protozoan PSR between the three troops (Buffels Bay, Cape Point, and Kanonkop) that live within the CoGH section of the TMNP (Figure 6.2).

Trichuris sp. and *Oesophagostomum* sp. were the only nematodes found in all study troops (Figure 6.3). *Trichostrongylus* sp. was found in all troops except Tokai. *Physaloptera* sp. was absent from both the Tokai and Cape Point troops. *Ascaris* sp. was absent from one troop only, namely, Buffels Bay. Hookworm type was only found in the Buffels Bay and Da Gama Park troops, and the unidentified spirurid was only found in the Kanonkop troop.

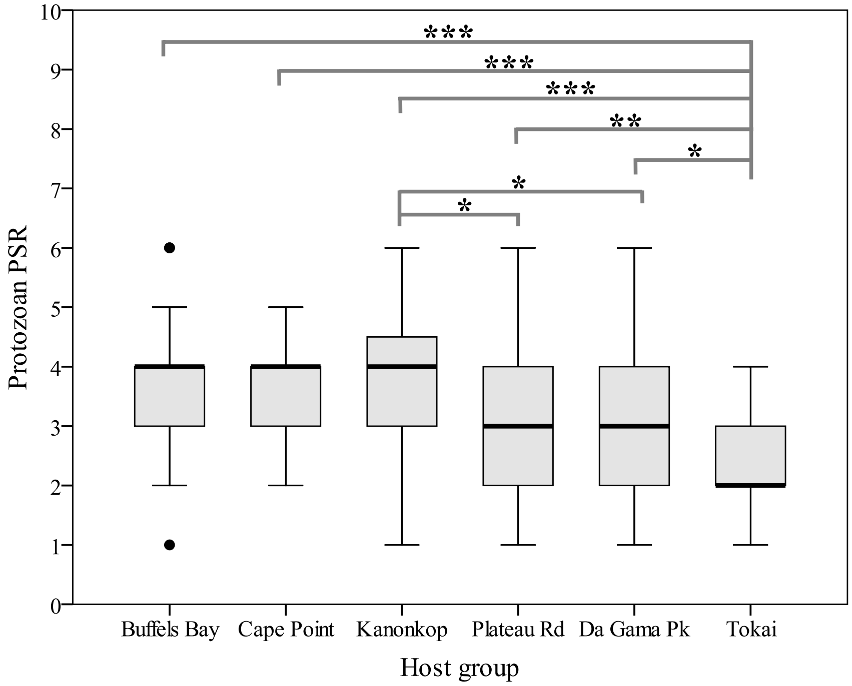


Figure 6.2 Protozoan species richness per host troop. The boxes show the interquartile ranges, bold horizontal bars show the median. The ends of the 'whiskers' represent the minimum and maximum values that are not outliers. Outliers: circles and stars. Asterisks indicate statistical differences between groups: Mann-Whitney U test: *p≤ 0.05; **p≤ 0.01; ***p≤ 0.001.

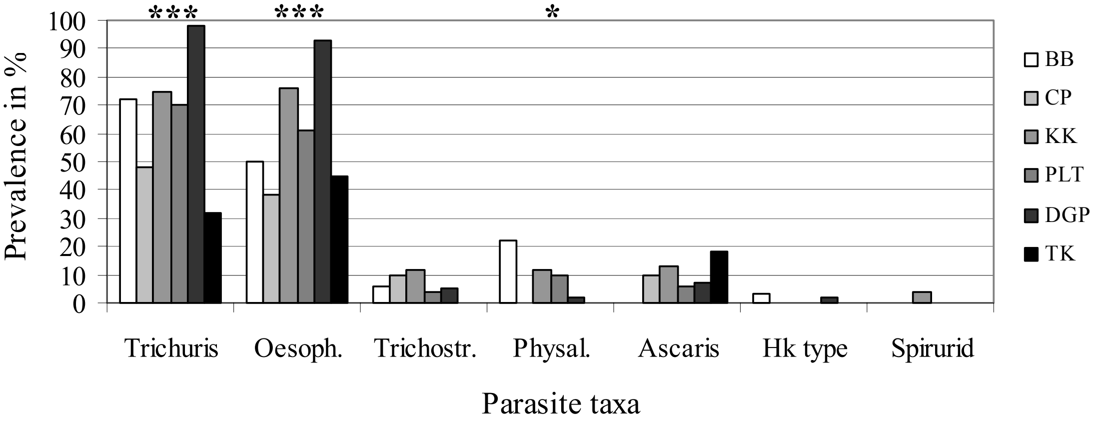


Figure 6.3 Prevalences of helminth taxa per baboon troops. Bars denote prevalence per parasite species for all host groups. Asterisks indicate statistical differences between groups: Pearson Chi-square: *p≤ 0.05; ***p≤ 0.001. BB=Buffels Bay (*n*=36), CP=Cape Point (*n*=21), KK=Kanonkop (*n*=68), PLT=Plateau Road (*n*=83), DGP=Da Gama Park (*n*=41), TK=Tokai (*n*=22). (Trichuris=*Trichuris* sp., Oesoph.=*Oesophagostomum* sp., Trichostr.=*Trichostrongylus* sp., Physal.=*Physaloptera* sp., Ascaris=*Ascaris* sp., Hk =hookworm).

The prevalence of *Trichuris* sp., *Oesophagostomum* sp., and *Physaloptera* sp. varied significantly between the six troops (Pearson Chi-square: *Trichuris* sp. Chi-square=36.517, df=5, p<0.001; *Oesophagostomum* sp. Chi-square=32.264, df=5, p<0.001; *Physaloptera* sp. Chi-square=14.427, df=5, p=0.013; see asterisks in Figure 6.3). The prevalence of the other nematodes did not vary significantly among the troops.

Appendix F reports the results of Mann-Whitney U tests for the comparison of prevalences of each parasite taxa between each study troop. *Trichuris* sp. and *Oesophagostomum* sp. varied the most across the six troops and were significantly higher in Da Gama Park than in all the other troops. The prevalence of *Trichuris* was significantly lower in Tokai compared to all other troops, except the Cape Point troop. The prevalence of *Oesophagostomum* sp. was significantly higher in Tokai compared to both the Kanonkop and Da Gama Park troops.

Among the protozoa, the prevalence of *Entamoeba chattoni*, *E. hartmanni*, and *Iodamoeba butschlii*, all usually non pathogenic, varied significantly among troops (Pearson Chi-square: *Entamoeba chattoni* Chi-square=13.195, df=5, p=0.022; *E. hartmanni* Chi-square=18.688, df=5, p=0.002; *Iodamoeba butschlii* Chi-square=30.627, df=5, p<0.001; see asterisks in Figure 6.4) being significantly lower in the Tokai troop (Appendix F).

6.2 Troop attributes and parasite infections

6.2.1 Correlations between troop attributes

Twelve troop attributes were measured and analyzed for possible association with parasite infection variations between the six Cape Peninsula troops. The value of each attribute for each troop is shown in Table 6.1. Mean troop size was 46 individuals (range=11-122). Mean host density was 4.44 individuals/km^2 and ranged from 1.12 to 12.44 baboons/km^2. Mean home-range size was 13.42 km^2 and ranged from 5.63 km^2 for Buffels Bay troop to 37.65 km^2 for Kanonkop.

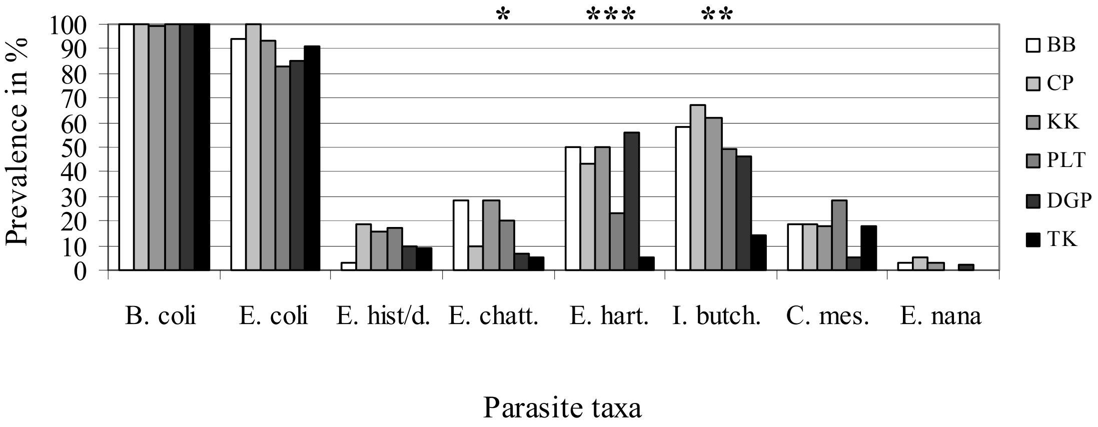


Figure 6.4 Prevalences of protozoan taxa per baboon troop. Bars denote prevalence per parasite species for all host groups. Asterisks indicate statistical differences between groups: Pearson Chi-square: *p≤ 0.05; ** p≤ 0.01; ***p≤ 0.001. BB=Buffels Bay (*n*=36), CP=Cape Point (*n*=21), KK=Kanonkop (*n*=68), PLT=Plateau Road (*n*=83), DGP=Da Gama Park (*n*=41), TK=Tokai (*n*=22). (B. coli=*Balantidium coli*, E. coli=*Entamoeba coli*, E. hist/d.=*E. histolytica/dispar*, E. chatt.=*E. chattoni*, E. hart.= *E. hartmanni*, I. butch.=*Iodamoeba butschlii*, C. mesn.=*Chilomastix mesnili*; E. nana=*Endolimax nana*).

The intensity of use of the home range varied between 6 % for Kanonkop to 62 % for Buffels Bay troop, with an average of 28 %. The number of troops that had home ranges overlapping with another troop ranged between zero and four, while the percentage of overlapping home range between a troop and its neighbouring troops varied from 0 % to 67.28 %, with an average of 23.16 % of shared home range. Mean percentage of home-range overlap with urban land was 3.5 % and varied from values close to 0 % for Kanonkop and Plateau Road to a higher value of 13.4 % for an urban troop like Da Gama Park. Mean percentage of home-range overlap with transformed land was 23.30 % and values ranged from a very low percentage overlap for the Kanonkop troop (0.50 %) to a very high percentage overlap for Tokai (92.70 %). Monitors were present in three of the six study troops, namely Cape Point, Da Gama Park, and Tokai. The number of sleeping sites varied from two to 18 sites, with an average of 10 per troop. In the absence of empirical data on the proportion of human food included in the diet of each troop, a broad index was used based on long-term observations of the frequency of raiding human food for each troop. This proportion ranged from very low (for Kanonkop troop, feeding only on natural resources) to medium (Plateau Road and Tokai troops, with some access to food of human origin) and high (for the urban-ranging troop Da Gama Park and the two troops in the nature reserve, Buffels Bay and Cape Point, that obtained a fair portion of their diet from the raiding of human food). Annual precipitation during the study period (average between 2006 and 2007) also varied across the Peninsula from the lowest values in the park (363.2 mm) to the highest (1276.8 mm) in the Tokai plantation. The average annual rainfall across the Peninsula was 577.6 mm.

Table 6.1 Ecological attributes of the six Cape Peninsula baboon study troops. HR = home range; Transf. = transformed land. See Literature Review and Methods for details on the various attributes.

Troop	Group size	Host density	HR Size (km^2)	% HR Use Intensity	No. Overlap. Troops	% HR Overlap. Troops	% HR Overlap. Urban	% HR Overlap Transf.	Monitors Presence	No. Sleeping Sites	Proportion Human Food	Rainfall (mm)
Buffels Bay	11	1.95	5.63	62	2	67.28	0.80	4.90	0	2	3	363.2
Cape Point	25	3.35	7.46	30	2	15.38	0.50	1.30	1	5	3	363.2
Kanonkop	42	1.12	37.65	6	4	4.31	0.10	0.50	0	15	1	363.2
Plateau Road	40	4.33	9.23	24	1	1.95	0.00	25.80	0	10	2	487.6
Da Gama Park	37	3.45	10.73	21	1	50.00	13.40	14.80	1	12	3	611.9
Tokai	122	12.44	9.81	23	0	0.00	6.00	92.70	1	18	2	1276.8
Average	46	4.44	13.42	28	2	23.16	3.50	23.30	n/a	10	n/a	577.6

In order to analyse the relationship between these independent variables, the Spearman's Rank Correlation Coefficient (r_s) was calculated. A table of correlations between attributes is provided in Appendix G. Most variables showed at least one significant correlation with other variables. Home-range size was negatively correlated with the intensity of home-range use (n=6, r_s=-1.000, p<0.001). The number of sleeping sites was positively correlated with group size (n=6, r_s=0.943, p=0.005) Host density correlated negatively with the number of overlapping troops (n=6, r_s=-0.971, p=0.001) and positively with the percentage of home range overlapping transformed land (n=6, r_s=0.943, p=0.002). See Appendix G for other significant correlations between variables.

6.2.2 Correlations between helminth prevalences

The infective stages of *Trichuris* sp., *Oesophagostomum* sp., *Trichostrongylus* sp., and *Ascaris* sp. all need to be ingested by the host, while hookworm larvae can infect hosts either by ingestion or skin penetration. The prevalences of each of these nematodes are shown in Table 6.2, as well as in Figure 6.3. Mean prevalence of *Trichuris* sp. among troops was 66 %; mean prevalence of *Oesophagostomum* sp. was 61 %; that of *Trichostrongylus* sp. was 6 %; the mean prevalence of *Ascaris* sp. was 9 % and the mean prevalence of hookworm type was 1 %. Collectively, the prevalence of all nematodes considered for the following analysis was 142 % and ranged from 95 to 205 %.

Table 6.2 Prevalence (%) of nematode infections in the Cape Peninsula baboon troops (only the nematodes that were used in the correlation matrix are represented here). (*Oesoph.=Oesophagostomum*, *Trichostr.=Trichostrongylus*).

Troop	*n*	*Trichuris* sp.	*Oesoph.* sp.	*Trichostr.* sp.	*Ascaris* sp.	Hookworm type	Collective
Buffels Bay	36	72	50	6	0	3	131
Cape Point	21	48	38	10	10	0	106
Kanonkop	68	75	76	12	13	0	176
Plateau Road	83	70	61	4	6	0	141
Da Gama Park	41	98	93	5	7	2	205
Tokai	22	32	45	0	18	0	95
Average	45	66	61	6	9	1	142

The Spearman's Rank Correlation Coefficient was used to explore the relationship between the respective prevalences of the different nematode species. Results are provided in Appendix H. Prevalences of *Trichuris* sp. and *Oesophagostomum* sp. were significantly positively correlated (*n*=6, r_s=-0.886, p=0.009). Prevalences between the other nematode species showed a positive (not significant) association, with the exception of *Ascaris* sp.. Prevalences of *Ascaris* sp. were negatively correlated (but not significantly) to the other nematode taxa, except the spirurid (which was not included in the following analysis). Prevalence of hookworm type and spirurid were also negatively correlated.

6.2.3 Correlations between troop attributes and parasite infections

The results of Spearman Rank correlation between troop attributes and PSR and prevalences are presented in the matrix in Table 6.3. In general, none of the troop attributes followed a clear pattern of correlation with the indices of parasite infection measured. Group size, host density, home-range size, and intensity of use of the home range correlated positively and negatively (not significantly) with most of the indices of parasite infection. Only two of these associations were significant and negative (Table 6.3).

Protozoan taxon diversity was significantly positively correlated to the number of neighbouring troops, and so was *Trichostrongylus* sp. prevalence. The percentage of overlap of home ranges with transformed land correlated significantly negatively with protozoan PSR and *Trichostrongylus* sp. prevalence. The degree of interaction with humans did not show any association with PSR and prevalence. Monitor presence was mostly negatively associated (not significantly) with parasitic infection, except for *Ascaris* sp.. No clear patterns (according to or against predictions) were found between indices of parasite infection and the number of sleeping sites, the proportion of human food in the diet and rainfall. Rainfall showed a significant negative correlation with protozoan PSR.

Table 6.3 Matrix of correlations between ecological attributes of baboon troops in the Cape Peninsula and diversity and prevalence of parasites identified in their respective troop members. Spearman's Rank correlation, *n*=6. Bold: significant after implementing false discovery rate control (Narum 2006). (*Oesoph.*=*Oesophagostomum* sp., *Trichostr.*=*Trichostrongylus* sp., Hookw.=hookworm type; HR=home range, Transf.=transformed)

Attributes		Helm. PSR	Prot. PSR	*Trichuris*	*Oesoph.*	*Trichostr.*	*Ascaris*	Hookw.	Collective
Group size	r_s	0.093	-0.617	-0.257	0.143	-0.371	0.771	-0.676	-0.086
	p	0.431	0.096	0.311	0.394	0.234	0.036	0.070	0.436
Host density	r_s	-0.247	-0.926	-0.543	-0.200	-0.943	0.200	-0.270	-0.371
	p	0.319	**0.004**	0.133	0.352	**0.002**	0.352	0.302	0.234
HR Size	r_s	0.525	-0.278	0.429	0.657	0.086	0.600	-0.338	0.543
	p	0.143	0.297	0.198	0.078	0.436	0.104	0.256	0.133
HR Use Intensity	r_s	-0.525	0.278	-0.429	-0.657	-0.086	-0.600	0.338	-0.543
	p	0.143	0.297	0.198	0.078	0.436	0.104	0.256	0.133
No. Overlap. Troops	r_s	0.207	0.953	0.412	0.088	0.971	-0.147	0.070	0.294
	p	0.347	**0.002**	0.209	0.434	**≤0.001**	0.390	0.448	0.286
HR Overlap. Troops	r_s	0.123	0.617	0.600	0.200	0.486	-0.657	0.845	0.371
	p	0.408	0.096	0.104	0.352	0.164	0.078	0.017	0.234
HR Overlap. Urban	r_s	-0.278	-0.370	0.143	0.086	-0.314	0.143	0.541	-0.029
	p	0.297	0.235	0.394	0.436	0.272	0.394	0.134	0.479
HR Overlap. Transf. Land	r_s	-0.154	-0.926	-0.429	-0.086	-1.000	0.029	-0.034	-0.314
	p	0.385	**0.004**	0.198	0.436	**≤0.001**	0.479	0.475	0.272
Monitors' Presence	r_s	-0.527	-0.422	-0.293	-0.293	-0.293	0.488	-0.115	-0.293
	p	0.141	0.203	0.287	0.287	0.287	0.163	0.414	0.287
No. Sleep Sites	r_s	0.093	-0.617	-0.086	0.257	-0.314	0.829	-0.507	0.029
	p	0.431	0.096	0.436	0.311	0.272	0.021	0.152	0.479
Proportion Human Food	r_s			0.093	-0.216	0.000	-0.525	0.657	-0.062
	p			0.431	0.341	0.500	0.143	0.078	0.454
Rainfall	r_s	-0.033	-0.984	-0.213	0.152	-0.880	0.334	-0.108	-0.091
	p	0.475	**≤0.001**	0.343	0.387	0.010	0.259	0.419	0.432

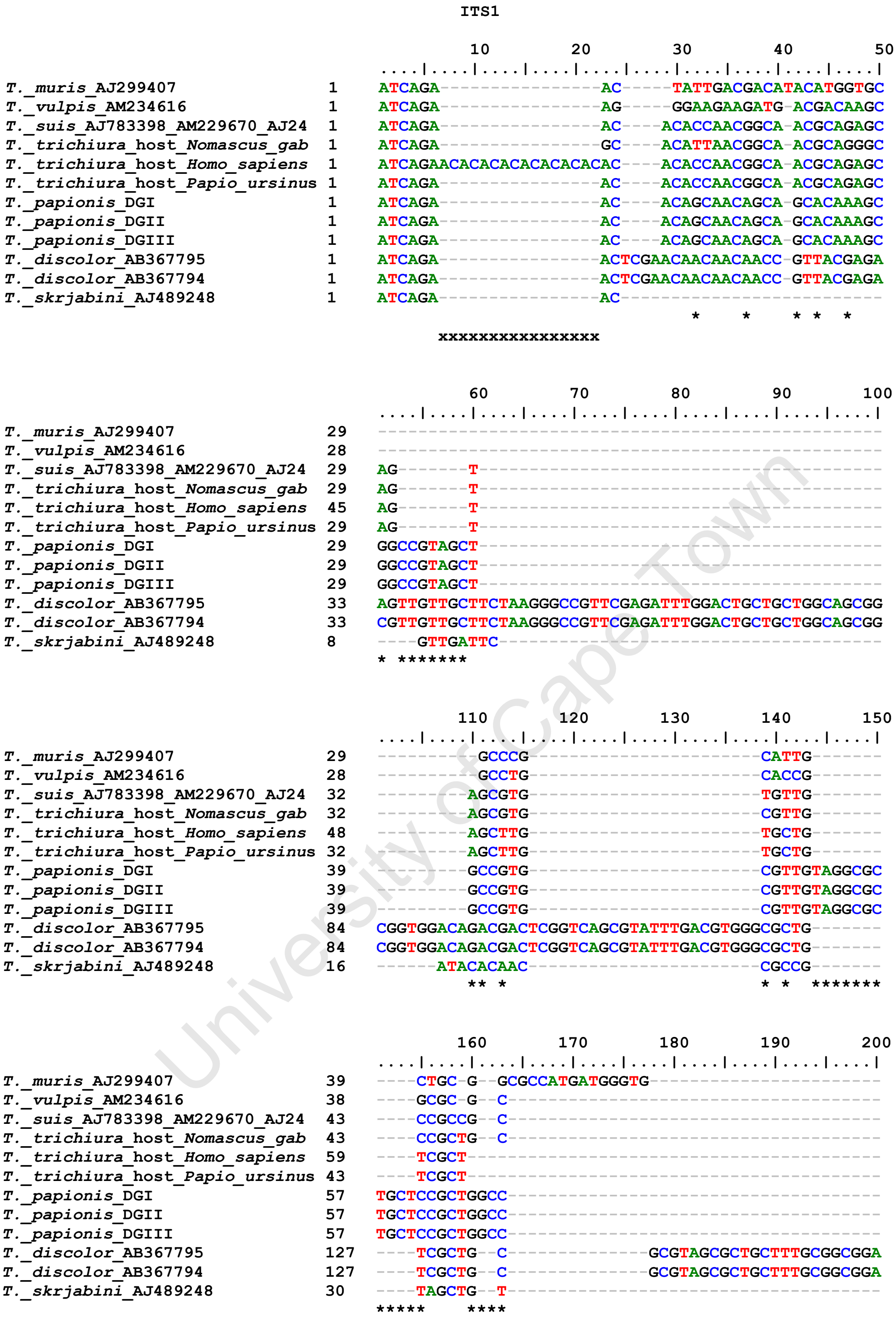
CHAPTER SEVEN

HOST SPECIFICITY: *TRICHURIS* SP.

An initial inspection of the nucleotide sequences showed that the ITS1-5.8S rDNA-ITS2 regions isolated from the *Trichuris* nematodes dissected from the guts of the Cape Point (CP) and Groot Olifantsbos (GOB) baboons were identical. The sequences from the two nematodes were therefore treated as one sequence (host: CP_GOB) (Table 3.6). The lengths of the ITS1 and ITS2 sequences of were 641 bp and 567 bp, respectively (Figure 7.1).

The Da Gama Park (DGI, DGII, and DGIII) *Trichuris* isolates presented differences in the length of the ITS1 (621 bp, 612 bp, and 609 bp, respectively) and ITS2 (522 bp, 522 bp, and 519 bp, respectively) sequences. The 5.8S rDNA gene was 154 bp in length for the *Trichuris* of all three isolates. Differences in length of the ITS sequences were due to both indels at positions 400, 449, 616-617, and 1035 of the ITS1 sequences, and repetitive nucleotide sequences, termed "microsatellites", found in the ITS1 sequences in positions 261 (CAG), 269 (GCA), and 492 (CGG) and in ITS2 sequences in position 1951 (ACG) (differences are annotated in Figure 7.1). Based on these analyses, the three DGI, DGII, and DGIII isolates were considered similar and most likely corresponding to the same species, with the differences described above corresponding to polymorphisms within the population.

The ITS1-5.8S rDNA-ITS2 sequences of *T. trichiura* isolated from human (*Homo sapiens*) patients from Cameroon showed clear differences to those of the *Trichuris* isolated from Da Gama Park baboons. While the length of the 5.8S rDNA gene remained identical (154 bp), the ITS1 and ITS2 sequences of *T. trichiura*, 670 bp and 593 bp, respectively, contained more nucleotides compared to the *Trichuris* isolated from DGI, DGII, and DGIII (Figure 7.1).



```
                                             ITS1

                                             10        20        30        40        50
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               1    ATCAGA----------------AC-----TATTGACGACATACATGGTGC
T._vulpis_AM234616              1    ATCAGA----------------AG-----GGAAGAAGATG-ACGACAAGC
T._suis_AJ783398_AM229670_AJ24  1    ATCAGA----------------AC----ACACCAACGGCA-ACGCAGAGC
T._trichiura_host_Nomascus_gab  1    ATCAGA----------------GC----ACATTAACGGCA-ACGCAGGGC
T._trichiura_host_Homo_sapiens  1    ATCAGAACACACACACACACACAC----ACACCAACGGCA-ACGCAGAGC
T._trichiura_host_Papio_ursinus 1    ATCAGA----------------AC----ACACCAACGGCA-ACGCAGAGC
T._papionis_DGI                 1    ATCAGA----------------AC----ACAGCAACAGCA-GCACAAAGC
T._papionis_DGII                1    ATCAGA----------------AC----ACAGCAACAGCA-GCACAAAGC
T._papionis_DGIII               1    ATCAGA----------------AC----ACAGCAACAGCA-GCACAAAGC
T._discolor_AB367795            1    ATCAGA----------------ACTCGAACAACAACAACC-GTTACGAGA
T._discolor_AB367794            1    ATCAGA----------------ACTCGAACAACAACAACC-GTTACGAGA
T._skrjabini_AJ489248           1    ATCAGA----------------AC--------------------------
                                                                    *    *    * *  *
                                           xxxxxxxxxxxxxxxx


                                             60        70        80        90       100
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               29   --------------------------------------------------
T._vulpis_AM234616              28   --------------------------------------------------
T._suis_AJ783398_AM229670_AJ24  29   AG-------T----------------------------------------
T._trichiura_host_Nomascus_gab  29   AG-------T----------------------------------------
T._trichiura_host_Homo_sapiens  45   AG-------T----------------------------------------
T._trichiura_host_Papio_ursinus 29   AG-------T----------------------------------------
T._papionis_DGI                 29   GGCCGTAGCT----------------------------------------
T._papionis_DGII                29   GGCCGTAGCT----------------------------------------
T._papionis_DGIII               29   GGCCGTAGCT----------------------------------------
T._discolor_AB367795            33   AGTTGTTGCTTCTAAGGGCCGTTCGAGATTTGGACTGCTGCTGGCAGCGG
T._discolor_AB367794            33   CGTTGTTGCTTCTAAGGGCCGTTCGAGATTTGGACTGCTGCTGGCAGCGG
T._skrjabini_AJ489248           8    ----GTTGATTC--------------------------------------
                                     * *******


                                            110       120       130       140       150
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               29   ----------GCCCG-----------------------CATTG-------
T._vulpis_AM234616              28   ----------GCCTG-----------------------CACCG-------
T._suis_AJ783398_AM229670_AJ24  32   ---------AGCGTG-----------------------TGTTG-------
T._trichiura_host_Nomascus_gab  32   ---------AGCGTG-----------------------CGTTG-------
T._trichiura_host_Homo_sapiens  48   ---------AGCTTG-----------------------TGCTG-------
T._trichiura_host_Papio_ursinus 32   ---------AGCTTG-----------------------TGCTG-------
T._papionis_DGI                 39   ---------GCCGTG-----------------------CGTTGTAGGCGC
T._papionis_DGII                39   ---------GCCGTG-----------------------CGTTGTAGGCGC
T._papionis_DGIII               39   ---------GCCGTG-----------------------CGTTGTAGGCGC
T._discolor_AB367795            84   CGGTGGACAGACGACTCGGTCAGCGTATTTGACGTGGGCGCTG-------
T._discolor_AB367794            84   CGGTGGACAGACGACTCGGTCAGCGTATTTGACGTGGGCGCTG-------
T._skrjabini_AJ489248           16   ------ATACACAAC-----------------------CGCCG-------
                                              ** *                         * *  *******


                                            160       170       180       190       200
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               39   ----CTGC-G--GCGCCATGATGGGTG-----------------------
T._vulpis_AM234616              38   ----GCGC-G--C-------------------------------------
T._suis_AJ783398_AM229670_AJ24  43   ----CCGCCG--C-------------------------------------
T._trichiura_host_Nomascus_gab  43   ----CCGCTG--C-------------------------------------
T._trichiura_host_Homo_sapiens  59   ----TCGCT-----------------------------------------
T._trichiura_host_Papio_ursinus 43   ----TCGCT-----------------------------------------
T._papionis_DGI                 57   TGCTCCGCTGGCC-------------------------------------
T._papionis_DGII                57   TGCTCCGCTGGCC-------------------------------------
T._papionis_DGIII               57   TGCTCCGCTGGCC-------------------------------------
T._discolor_AB367795            127  ----TCGCTG--C--------------GCGTAGCGCTGCTTTGCGGCGGA
T._discolor_AB367794            127  ----TCGCTG--C--------------GCGTAGCGCTGCTTTGCGGCGGA
T._skrjabini_AJ489248           30   ----TAGCTG--T-------------------------------------
                                     *****    ****
```

Figure 7.1 PRANK alignment of *Trichuris* ITS1-5.8 rDNA-ITS2 from various hosts (see Tables 3.6 and 3.7). Nucleotide differences between *T. papionis* from DGI, DGII and DGIII are marked with crosses; nucleotide differences between *T._trichiura*_host_*Papio_ursinus* (CP_GOB) and *T. trichiura*_host_*Homo_sapiens* are designated with x signs; nucleotide differences between *T. papionis* (DGI, DGII and DGIII) and *T._trichiura*_host_*Papio_ursinus* (CP_GOB) are indicated with asterisks.

```
                                             210       220       230       240       250
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               59   --------------CGCTT---------------------------GG--
T._vulpis_AM234616              44   --------------CGCTT---------------------------AG--
T._suis_AJ783398_AM229670_AJ24  50   --------------TGCTTGC-------------------------AGCA
T._trichiura_host_Nomascus_gab  50   --------------TGCTTGC-------------------------GGCG
T._trichiura_host_Homo_sapiens  64   -----------------------------------------------GCA
T._trichiura_host_Papio_ursinus 48   -----------------------------------------------GCA
T._papionis_DGI                 70   --------------TGCTAGC-------------------------AGCA
T._papionis_DGII                70   --------------TGCTAGC-------------------------AGCA
T._papionis_DGIII               70   --------------TGCTAGC-------------------------AGCA
T._discolor_AB367795            157  ACTTCCTCGGCGGCTG-ATGTTTGCGAGCAGTATGGGACGTTGACGAG--
T._discolor_AB367794            157  ACTTCCTCGGCGGCTG-ATGTTTGCGAGCAGTATGGGACGTTGACGAG--
T._skrjabini_AJ489248           37   --------------TG-TTGT-------------------------AG--
                                                   *******                         *


                                             260       270       280       290       300
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               66   -----AGCTGCA-CAGC--ACCCTGCTGCTGCTG----------------
T._vulpis_AM234616              51   -----CGCGACA-GCGCGGAGCCTGCTGCTCGTG----------------
T._suis_AJ783398_AM229670_AJ24  61   GTAGCAGCAGCAGCAGCAGCGTCGGGTGCTGGTGACGACGCTCGTTCGTC
T._trichiura_host_Nomascus_gab  61   GCA------------------CAGGGTGCCGGTGAC---GCCCGTTTCTA
T._trichiura_host_Homo_sapiens  67   TCA------------------TCGGGTGCTGGTGAC---GCTCGTTGCTT
T._trichiura_host_Papio_ursinus 51   TCA------------------TCGGGTGCTGGTGAC---GCTCGTTGCTT
T._papionis_DGI                 81   GCAGCAGCAGCAGCAGCAGCAGCAGGCGCTGGTG----------------
T._papionis_DGII                81   GCAGCAGCAGCAGCAGCA------GGCGCTGGTG----------------
T._papionis_DGIII               81   GCAGCAGCAG---CAGCA------GGCGCTGGTG----------------
T._discolor_AB367795            204  -----GACGGCGGCGGCGACGTTAGCTCC--GTG----------------
T._discolor_AB367794            204  -----GACGGCGGCGGCGACGTTAGCTCC--GTG----------------
T._skrjabini_AJ489248           45   -----AGCGGCGGCA-----------------------------------
                                     *  ******************* *  *       **   ***********
                                               +++     ++++++


                                             310       320       330       340       350
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               92   --------CTAG-----CTGCA----------------------------
T._vulpis_AM234616              79   --------GTGG--------------------------------------
T._suis_AJ783398_AM229670_AJ24  112  CGGCATTG-TGGCGTGTTCGCA-------GTTGGCC-------GCCCC--
T._trichiura_host_Nomascus_gab  91   CGGC----------------------------------------------
T._trichiura_host_Homo_sapiens  97   CGGCAGTG-TGGCGT--TCACA-------GTCGGCC-------GC-----
T._trichiura_host_Papio_ursinus 81   CAGCAGTG-TGGCGT--TCGCA-------GTCGGCC-------GC-----
T._papionis_DGI                 115  ---------TGGCGT--TTGC-----------------------------
T._papionis_DGII                109  ---------TGGCGT--TTGC-----------------------------
T._papionis_DGIII               106  ---------TGGCGT--TTGC-----------------------------
T._discolor_AB367795            230  ---------TGG-----TTGCAAGCGCTAGTCGGCCCAGCATCGGCCGTC
T._discolor_AB367794            230  ---------TGG-----TTGCAAGCGCTAGTCGGCCCAGCATCGGCCGTC
T._skrjabini_AJ489248           55   ------------------TGCA-------GTCGGCC-------GGCCAGC
                                     ********          *  *       *******       **


                                             360       370       380       390       400
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               101  --------TGGT--------------------------------------
T._vulpis_AM234616              83   --------------------------------------------------
T._suis_AJ783398_AM229670_AJ24  145  -GTA-CTTGGGCGCG---------------------ACGTGAGCGCGCGT
T._trichiura_host_Nomascus_gab  95   ---------GGCGCG---------------------ACGTGAGCGCGCGT
T._trichiura_host_Homo_sapiens  125  -GTA-CTTTGGCTCG---------------------ACATGAGCGCGCGT
T._trichiura_host_Papio_ursinus 109  -GTA-CTTCGGCTCG---------------------ACACGAGCGCGCGT
T._papionis_DGI                 125  -------TCGGTCCG---------------------ATGCGAGC------
T._papionis_DGII                119  -------TCGGTCCG---------------------ATGCGAGC------
T._papionis_DGIII               116  -------TCGGTCCG---------------------ATGCGAGC------
T._discolor_AB367795            266  GATAACTGAGCTTGCTTTCTACCGTGAGCTTTCACCACCGCAGC------
T._discolor_AB367794            266  GATAACTGAGCTTGCTTTCTACCGTGAGCTTTCACCACCGCAGC------
T._skrjabini_AJ489248           73   GGTA-CTTCGCTGGC---------------------AGCGATGC------
                                      *** **    **                        **     ******
                                             x                              x
```

Figure 7.1 continued

```
                                            410       420       430       440       450
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               105  -------------------------------------------------C
T._vulpis_AM234616              83   --------------------------------------------------
T._suis_AJ783398_AM229670_AJ24  172  TGCCACTGC---CGTGAGCAGCGTCCACCGTTGC---ACCACCA------
T._trichiura_host_Nomascus_gab  115  TGCCACTGC---CGAGAGCAGCGTCCACCGTTGC---ACCA---------
T._trichiura_host_Homo_sapiens  152  TGCCGCTGCCGAGGAGAACGGCGTGCACGGTTGCAGCACCA---------
T._trichiura_host_Papio_ursinus 136  TGCCGCTGCTGCCGAGAACAGCGTGCACCGTTGC---ACCA---------
T._papionis_DGI                 141  -------------------AACGTCCGCCG-------GCCT---------
T._papionis_DGII                135  -------------------AACGTCCGCCG-------GCTT---------
T._papionis_DGIII               132  -------------------AACGTCCGCCG-------GCTT---------
T._discolor_AB367795            310  -------------------A-TGTTCGCCCTTGT---TCTA---CCATGC
T._discolor_AB367794            310  -------------------A-TGTTCGCCCTTGT---TCTA---CCATGC
T._skrjabini_AJ489248           95   -------------------A-TGAATGC------------------ATGC
                                     ******************* *   * *   ****   * **
                                              x xx      x        x     xxx  +


                                            460       470       480       490       500
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               106  TGCGTCC---ATGTCCAGATCT---------------AC-----------
T._vulpis_AM234616              83   TGCG--C---ACGTCCAGGTCT-GCCG----------GC-----------
T._suis_AJ783398_AM229670_AJ24  210  ---C--C---ACTTCCAGATCC-CAAGCGC--AGGCCGCGCTGGCTACGG
T._trichiura_host_Nomascus_gab  150  ---G--C---AGTTCCAGATCC-GAAGAGC--AGGTCGCGCTGACCACGG
T._trichiura_host_Homo_sapiens  193  ---G--C---ACTTCCAGATCC-GAAGAGC--AGGCCGCGCTGGCTACGG
T._trichiura_host_Papio_ursinus 174  ---G--C---ACTTCCAGATCC-GAAGAGC--AGGCCGCGCTTGCTACGG
T._papionis_DGI                 156  ---A--C---AGTTCCAGGTCT-GAAGAGCGCAGGCGGCGGCGGCT-CGT
T._papionis_DGII                150  ---A--C---AGTTCCAGGTCT-GAAGAGCGCAGGCGGCGG---CT-CGT
T._papionis_DGIII               147  ---A--C---AGTTCCAGGTCT-GAAGAGCGCAGGCGGCGG---CT-CGT
T._discolor_AB367795            334  TGCT--T---ACTTCCAGATCT-TAAG----------GCGAACGCTCCCG
T._discolor_AB367794            334  TGCT--T---ACTTCCAGATCT-TAAG----------GCGAACGCTCCCG
T._skrjabini_AJ489248           107  TGCG--CGCAACTTCCAGATCTCTGCG----------GAGGAG----CGA
                                        *       *      *  *        **    *   ***   *  *
                                                                              x
                                                                             +++


                                            510       520       530       540       550
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               127  --------------------------------------------------
T._vulpis_AM234616              106  --------------------------------------------------
T._suis_AJ783398_AM229670_AJ24  249  TCGTCCTGCGCCGCTTGAC----TCGG--------------------TGA
T._trichiura_host_Nomascus_gab  189  TCGACCTGCGCCGCTCGAC----ACGG--------------------TGA
T._trichiura_host_Homo_sapiens  232  TCGTCCCGCGCTGCTCGACGACTAC-G--------------------TGG
T._trichiura_host_Papio_ursinus 213  TCGTCCCGCGCTGCTCGACGACTAC-G--------------------CGG
T._papionis_DGI                 197  TCCGCC--CGGCGGGCGAG----TCGT--------------------CGA
T._papionis_DGII                188  TCCGCC--CGGCGGGCGAG----TCGT--------------------CCA
T._papionis_DGIII               185  TCCGCC--CGGCGGGCGAG----TCGT--------------------CGA
T._discolor_AB367795            369  TTATCA--CCAGGCAAGCT----CGGCAAGCATGGTACGCGATCAACCGT
T._discolor_AB367794            369  TTATCA--CCAGGCAAGCT----CGGCAAGCATGGTACGCGATCAACCGT
T._skrjabini_AJ489248           142  TTCTCC--CGCGGGGAGAC----CGGC--------------------CGT
                                       **  **  ** **   ****** **                      *
                                                                                    x+


                                            560       570       580       590       600
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               127  ----------ATC-------------------------AG-------GCT
T._vulpis_AM234616              106  ----------CTG-------------------------CG-------GCC
T._suis_AJ783398_AM229670_AJ24  275  TCACCACCAGTACGACCGGCTGCAGACGGACGACTGCGTG-------GCT
T._trichiura_host_Nomascus_gab  215  CCACCAGCAGTACGGCCGGCTGCAGACGGACGACTGCGCG-------GCT
T._trichiura_host_Homo_sapiens  261  CTACCGCCAGTACGACCGGCTGCAGACGGACGACTGC-TGCTGCGTAGCT
T._trichiura_host_Papio_ursinus 242  CTACCGCCAGT-CGACCGGCTGCAGACGAACGACTGCGTA----GTAGCT
T._papionis_DGI                 221  TCGTCGCCGTCAC-------------------------CG-------GCT
T._papionis_DGII                212  TCGTCGCCGTCAC-------------------------CG-------GCT
T._papionis_DGIII               209  TCGTCGCCGTCAC-------------------------CG-------GCT
T._discolor_AB367795            413  TCAGCCTCAGCTG-------------------------CG-------GTC
T._discolor_AB367794            413  TCAGCCTCAGCTG-------------------------CG-------GTC
T._skrjabini_AJ489248           166  TCAGCCTCAGCTG-------------------------CG-------GCC
                                     ****    **** ***************************    ***
                                                x                x        x xxxxx
```

Figure 7.1 continued

```
                                            610       620       630       640       650
                                    ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               136 TGATGAATC-GTAGCGATGCTAC-----------AAC-T------CT---
T._vulpis_AM234616              115 GGTTGGGCC-GCGGCCGT-CGAC-----------ATTGT------GC---
T._suis_AJ783398_AM229670_AJ24  318 GAGTCAGTCGGCATCG-----TC-----------GCGGGACGTCCGTGCT
T._trichiura_host_Nomascus_gab  258 GAGTCAGCCAGCATCG-----TCGA------GCGGCCGGACGTCCGTGTT
T._trichiura_host_Homo_sapiens  310 CAGTCAGCTAGCACCA-----GC-ACCGGCAGCCGCTAGACGTCCGTGCT
T._trichiura_host_Papio_ursinus 287 CAGGCAGCTAGCACCA-----GC-A------GCCGCTAGGCGTCCGTGCT
T._papionis_DGI                 239 CGATCAGGCAGCAGCGGT-TTTC-----------ACTTG------CTGCT
T._papionis_DGII                230 CGATCAGGCAGCAGCAAT-TTTC-----------ACTTG------CTGCT
T._papionis_DGIII               227 CGATCAGGCAGCAGCAAT-TTTC-----------ACTTG------CTGCT
T._discolor_AB367795            431 GCGTAGCTCAGCTCCTGG-TGGC-----------AATGC------G-GTT
T._discolor_AB367794            431 GCGTAGCTCAGCTCCTGG-TGGC-----------AATGC------G-GTT
T._skrjabini_AJ489248           184 GGG--------------------------------AT-------------
                                     ***   **    * *** ***  *      ****  * *******
                                       x           ++        xxxxxx        x


                                            660       670       680       690       700
                                    ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               164 ------------------------AC---CGGTACCTGCTCCGTTTGGG-
T._vulpis_AM234616              143 ------------------------AC---CGGTACCTGCTCCGCTTGGG-
T._suis_AJ783398_AM229670_AJ24  352 TGCTC--GCCTGCCAACAACG---AC---CGGTACCTGTTCCGTCTGGG-
T._trichiura_host_Nomascus_gab  297 CCCGC--GCCTGCCAACAACGATGAC---CGGTACCTGCTCCGTCTGGG-
T._trichiura_host_Homo_sapiens  354 CGCGCGCGCCTGCCAACAACGATGAC---CGGTACCTGTTCCGTCTGGG-
T._trichiura_host_Papio_ursinus 325 CGCGC--GCCTGSCAACAACGATGAC---CGGTACCTGTTCCGTCTGGG-
T._papionis_DGI                 271 CGC-C--GCCTGCGCGCAGTC---AC---CGGTACCTGTTCCGTTGTGG-
T._papionis_DGII                262 CGC-C--GCCTGCGCGCAGTC---AC---CGGTACCTGTTCCGTTGTGG-
T._papionis_DGIII               259 CGC-C--GCCTGCGCGCAGTC---AC---CGGTACCTGTTCCGTTGTGG-
T._discolor_AB367795            462 AGCGC--GTTTATTCGCCTTG---ATAGACGGTACCTGTTCCGTTTGGG-
T._discolor_AB367794            462 AGCGC--GTTTATTCGCCTTG---ATAGACGGTACCTGTTCCGTTTGGG-
T._skrjabini_AJ489248           189 ----C--GTCTCTTC-----G---ATTGACGGTACCTGTTCCGCTTGGGC
                                       *        ****  ******                    ***
                                         xx     x


                                            710       720       730       740       750
                                    ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               185 --CTCTTGTG---GCGGCAGTGTGGATCTGGCTGTCGCCGTGGCCGCCGG
T._vulpis_AM234616              164 --CTCCTGTG---GCGGCAGTGTGGATCTGGCTGTCGCCGTGGCCGCCGG
T._suis_AJ783398_AM229670_AJ24  392 --CCTCAGTGGCTGCGGCAGTGTGGATCTGGCTGCCGTTAGCGCCGCCGG
T._trichiura_host_Nomascus_gab  340 --CCTCAGTAGCTGCGGCAGTGTGGATCTGGCTGCCGTCAGCGCCGCCGG
T._trichiura_host_Homo_sapiens  399 --CCTCAGTAGCTGCGGCAGTGTGGATCTGGCTGCCGTCAGCGCCGCCGG
T._trichiura_host_Papio_ursinus 368 --CCTCAGTAGCTGCGGCAGTGTGGATCTGGCTGCCGTCAGCGCCGCCGG
T._papionis_DGI                 310 --CCTCCGTGGCTGCGGCAGTTTGGATCTGGCTGTCGTTAGCGCCGCCGG
T._papionis_DGII                301 --CCTCCGTGGCTGCGGCAGTTTGGATCTGGCTGTCGTTAGCGCCGCCGG
T._papionis_DGIII               298 --CCTCCGTGGCTGCGGCAGTTTGGATCTGGCTGTCGTTAGCGCCGCCGG
T._discolor_AB367795            505 --CTTCACTGGCAGCGGCAGTGTAGATCTGGCTGTCGCTTGCGCCGCCGG
T._discolor_AB367794            505 --CTTCACTGGCAGCGGCAGTGTAGATCTGGCTGTCGCTTGCGCCGCCGG
T._skrjabini_AJ489248           225 ACCTTGACCAGCAGCGGCAGTGTGGATCTGGCTGTCGCTTGCGCCGCCGG
                                          *  *           *            *   *


                                            760       770       780       790       800
                                    ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               230 TTGCAATCTCTCT------CTCTG-T---GTGGTGTGTCATCGGT-----
T._vulpis_AM234616              209 TGGCAGTCTCGCT-------------------------------------
T._suis_AJ783398_AM229670_AJ24  440 TTGCAGCCGACCG------TGCTGCT---GCGGGTTTTCATCACGT---C
T._trichiura_host_Nomascus_gab  388 TTGCAGCCGACCG------TGCCGTC---GCGAGCTGTCATCACGT---C
T._trichiura_host_Homo_sapiens  447 TTGCAACCGACCG------TGCTGCT---GCGGGCTGTCATCACGT---C
T._trichiura_host_Papio_ursinus 416 TTGCAACCGACCT------TGCTGCT---GCGGGCTGTCATCACGT---C
T._papionis_DGI                 358 TTGCAGTCGACCG------TGCTGCC---CCG---------CCAGT---A
T._papionis_DGII                349 TTGCAGTCGACCG------TGCTGCC---CCG---------CCAGT---A
T._papionis_DGIII               346 TTGCAGTCGACCG------TGCTGCC---CCG---------CCAGT---A
T._discolor_AB367795            553 TTGCAGACGACTG------CGCTGCTTCA--GTTCCGTGCTCAGCTTCGA
T._discolor_AB367794            553 TTGCAGACGACTG------CGCTGCTTCA--GTTCCGTGCTCAGCTTCGA
T._skrjabini_AJ489248           275 TTGGAGACGGCCAAGCCGCCGCTGCGTAACCGCTCCGTGCTCCGTTGCGA
                                         **     *            *   *  ********* **     *
                                                x
```

Figure 7.1 continued

```
                                            810       820       830       840       850
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               265  ----------------------------------------GACCACCA--
T._vulpis_AM234616              222  --------------------------------------------------
T._suis_AJ783398_AM229670_AJ24  478  ---------GCCGAGC-CCCCCGGTGG-CGTC----GATGAAGCGGCA-T
T._trichiura_host_Nomascus_gab  426  ---------GCCGACCGCTCCCGGTGG-CGTT----GATGAAGCGGCG--
T._trichiura_host_Homo_sapiens  485  ---------GCCGACCGCCCCCGGTGG-CGTT----GATGATGCGGCAT-
T._trichiura_host_Papio_ursinus 454  ---------GCCGACCGCCCCCGGTGG-CGTT----GATGATGCGGCA--
T._papionis_DGI                 387  ---------GTTG--------CACTGG-CGCT----GAAGAAGCAGCG--
T._papionis_DGII                378  ---------GTTG--------CACTGG-CGCT----GAAGAAGCAGCG--
T._papionis_DGIII               375  ---------GTTG--------CACTGG-CGCT----GAAGAAGCAGCG--
T._discolor_AB367795            596  TGTATCTTCGGAG--------CGGAGA-CGCTACGATACGGACTGGCT--
T._discolor_AB367794            596  TGTATCTTCGGAG--------CGGAGA-CGCTACGATACGGACTGGCT--
T._skrjabini_AJ489248           324  ---------GCAG--------CAGAGAGCGGT----TACGG--CGGCT--
                                               ** ******** **      *       *  *  *  *
                                                                                    x

                                            860       870       880       890       900
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               273  GC---------AGGCGGTGATCAGGTTCAAAGAACGGGAG-T--CGGCAA
T._vulpis_AM234616              222  GC---------TGGGCGAGACCAGGTTCAAAGAACGGGAG-T--CGGCGG
T._suis_AJ783398_AM229670_AJ24  512  GC---------TA-TGTCGGTGAGGTTTAAAGAACGGCCGTT--CC---A
T._trichiura_host_Nomascus_gab  460  GCACGA-----CA-CGTCGGTGAGGTGTAAGGAACGGCCGTTCGCC---A
T._trichiura_host_Homo_sapiens  520  GC---------TA-TGTCGGTGAGGTTTAAAGAACGGCCGTTCGCC---T
T._trichiura_host_Papio_ursinus 488  GC---------TA-TGTCGGTGAGGTTTAAAGAACGGCCGTTCGCC---T
T._papionis_DGI                 413  GC---------TAGCGTCGACGAGGTTCAAAGAACAGCCGTT--CG---A
T._papionis_DGII                404  GC---------TAGCGTCGACGAGGTTCAAAGAACAGCCGTT--CG---A
T._papionis_DGIII               401  GC---------TAGCGTCGACGAGGTTCAAAGAACAGCCGTT--CG---A
T._discolor_AB367795            635  GC----GCGTATACGTTCGTCGAGGTTCAAAGAACGACTG-T--CG---A
T._discolor_AB367794            635  GC----GCGTATACGTTCGTCGAGGTTCAAAGAACGACTG-T--CG---A
T._skrjabini_AJ489248           349  GC----CCT----GGGCCGTCGAGGTTCAAAGAACGACTG-T--CG---C
                                                  **    **      *       *      ** *   *

                                            910       920       930       940       950
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               312  GCGTG-----------------CACGATGCTGACA-----GCTCGTCGCC
T._vulpis_AM234616              261  CGGCG--------GCCGACAACGACGCCGCCGACG-----GCTCGTCGCC
T._suis_AJ783398_AM229670_AJ24  548  ACTCG--------AGCG-CATCGAGGAACGCGACG-----GCTCGTCGCC
T._trichiura_host_Nomascus_gab  502  CCTTG--------AGCG-CACAAGAAAGCA--ACG-----GCTCGTCGCC
T._trichiura_host_Homo_sapiens  558  CCGTG--------AGCG-AATCGGGGAAGG--ACG-----GCTCGTCGCC
T._trichiura_host_Papio_ursinus 526  CCATG--------AGCG-AATCGGGGAAGG--ACG-----GCTCGTCGCC
T._papionis_DGI                 450  CCTCG--------AGC---ATCGAGGA------CG-----GCTCGTCGCC
T._papionis_DGII                441  CCTCG--------AGC---ATCGAGGA------CG-----GCTCGTCGCC
T._papionis_DGIII               438  CCTCG--------AGC---ATCGAGGA------CG-----GCTCGTCGCC
T._discolor_AB367795            675  GAGTGCGAGGCTTGGCG-CACC-----CTTCGACG-----GTTCGTCGCC
T._discolor_AB367794            675  GAGTGCGAGGCTTGGCG-CACC-----CTTCGACG-----GTTCGTCGCC
T._skrjabini_AJ489248           386  GCGCG--------GGCG-CTTC-----CCTCGTCGTGGCAGATCGTCGCC
                                       **            * *    *   ***  *
                                       x

                                            960       970       980       990      1000
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               340  GGTTGG-------------AG-------CAGTGCT---------------
T._vulpis_AM234616              298  GGTGTA-------------AG-------GCGGAGC---------------
T._suis_AJ783398_AM229670_AJ24  584  GGTTGG-------------AT-------CTTCGTTATTA-----------
T._trichiura_host_Nomascus_gab  536  GGTTGG-------------AT-------CTCCGTTT--------------
T._trichiura_host_Homo_sapiens  592  GGTTGG-------------AT-------CTTCCTAA--------------
T._trichiura_host_Papio_ursinus 560  GGTTGG-------------AT-------CTTCGTTC--------------
T._papionis_DGI                 478  GGTTGGAAAAAGAAAAAGCAG-------CTTCACCAGTGCACAAGGCGTC
T._papionis_DGII                469  GGTTGGAAAAAGAAAAAGCAG-------CTTCACCAGTGCACAAGGCGTC
T._papionis_DGIII               466  GGTTGGAAAAAGAAAAAGCAG-------CTTCACCAGTGCACAAGGCGTC
T._discolor_AB367795            714  GTCTGG-------------ACCAGTACATTTCGGT---------------
T._discolor_AB367794            714  GTCTGG-------------ACCAGTACATTTCGGT---------------
T._skrjabini_AJ489248           422  GTCTGG-------------AC-------TTTTGGT---------------
                                           ************* *           ******************
                                                                     x xx
```

Figure 7.1 continued

```
                                            1010      1020      1030      1040      1050
                                    ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               354 ---------TGGC-GCAC-AGGCGGCAAC-AGGTCGG-----TC-GCTGA
T._vulpis_AM234616              312 ---------CGAC-CGAC-CGACGACAGT---GTCGG-----TCGGCTCC
T._suis_AJ783398_AM229670_AJ24  602 -----ACGACCAATGCAG-ATAAG----C---TGCGC-----TTCGTCGA
T._trichiura_host_Nomascus_gab  551 -----ACGACCAATGCAG-ATAAG----C---TGCGC-----TTCGCTGA
T._trichiura_host_Homo_sapiens  607 -----ATGACCAATGCAG-ATAAG----C---TGCGC-----TTCGCTGA
T._trichiura_host_Papio_ursinus 575 -----ATGACCAATGCAG-ATAAG----C---TGCGC-----TTCGCTGA
T._papionis_DGI                 521 GTCCTACTACGCACGCCG-ATGTG----CC--TTCGA-----CACGCAGA
T._papionis_DGII                512 GTCCTACTACGCACGCCG-ATGTG----CC--TTCGA-----CACGCAGA
T._papionis_DGIII               509 GTCCTACTACGCACGCCG-ATGTG----CC--TTTGA-----CACGCAGA
T._discolor_AB367795            735 ---------CCACTTCACTCTACG----C---AACAACAGCGTT------
T._discolor_AB367794            735 ---------CCACTTCACTCTACG----C---AACAACAGCGTT------
T._skrjabini_AJ489248           436 ---------CCACTTCAC-GTACA----C---TTCTA-----TC------
                                    ***** **  ** *  *    **      *   ** *     **   *
                                                                      +

                                            1060      1070      1080      1090      1100
                                    ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               386 GCACTGCTTACGTTGAAAAGAGAA---C-AAGCAAACTTTCGAATACA--
T._vulpis_AM234616              343 GCA------ACGAAAAAAAGAAGG---CTTAGAGAAAGTTCGAAAAAGTG
T._suis_AJ783398_AM229670_AJ24  634 --------------------AGTG---C-AGGAA------C----TCTTG
T._trichiura_host_Nomascus_gab  583 --------------------AGCG---C-AGGAA------CGAACTGTTG
T._trichiura_host_Homo_sapiens  639 --------------------AGCG---T-AGGAA------CGAATTGTTG
T._trichiura_host_Papio_ursinus 607 --------------------AGCGACGC-AGGAA------CGAATTGTTG
T._papionis_DGI                 559 -CACTGCTGTCGGCGCAATGAGCG---C-TAGTAGCA-TTCGAACTGCTG
T._papionis_DGII                550 -CACTGCTGTCGGCGCAATGAGCG---C-TAGTAGCA-TTCGAACTGCTG
T._papionis_DGIII               547 -CACTGCTGTCGGCGCAATGAGCG---C-TAGTAGCA-TTCGAACTGCTG
T._discolor_AB367795            763 ---------------------GCT---C-TGTACGAA-TTCGAACTGGGA
T._discolor_AB367794            763 ---------------------GCT---C-TGTACGAA-TTCGAACTGGGA
T._skrjabini_AJ489248           458 ---------------------GAT---C-T------A-TTCGAAAGAGTA
                                     *******************    **** ** * *** **    *  *
                                                            xxxx

                                            1110      1120      1130      1140      1150
                                    ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               430 -AAGACA-------------------------------------------
T._vulpis_AM234616              385 CTAGCTT-------------------------------------------
T._suis_AJ783398_AM229670_AJ24  651 AAACATG-------------------------------------------
T._trichiura_host_Nomascus_gab  604 AGCGATGATGCCGGTACCTGACCGTTCCGTCCGGGCCTCAGCGGCTGCGG
T._trichiura_host_Homo_sapiens  660 AACGATG-------------------------------------------
T._trichiura_host_Papio_ursinus 631 AACTACG-------------------------------------------
T._papionis_DGI                 603 CTGTACG-------------------------------------------
T._papionis_DGII                594 CTGTACG-------------------------------------------
T._papionis_DGIII               591 CTGTACG-------------------------------------------
T._discolor_AB367795            788 AAGCAAC-------------------------------------------
T._discolor_AB367794            788 AAGCAAC-------------------------------------------
T._skrjabini_AJ489248           477 AAGCAAC-------------------------------------------
                                    ***
                                       x x

                                           1160      1170      1180      1190      1200
                                    ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               436 --------------------------------------------------
T._vulpis_AM234616              392 --------------------------------------------------
T._suis_AJ783398_AM229670_AJ24  658 --------------------------------------------------
T._trichiura_host_Nomascus_gab  654 CAGCGTGGATCAGGCTGCCGTTAGCGCCGCCGGTTGCAGCCGACCGTGCC
T._trichiura_host_Homo_sapiens  667 --------------------------------------------------
T._trichiura_host_Papio_ursinus 638 --------------------------------------------------
T._papionis_DGI                 610 --------------------------------------------------
T._papionis_DGII                601 --------------------------------------------------
T._papionis_DGIII               598 --------------------------------------------------
T._discolor_AB367795            795 --------------------------------------------------
T._discolor_AB367794            795 --------------------------------------------------
T._skrjabini_AJ489248           484 --------------------------------------------------
```

Figure 7.1 continued

```
                                           1210      1220      1230      1240      1250
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               436  --------------------------------------------------
T._vulpis_AM234616              391  --------------------------------------------------
T._suis_AJ783398_AM229670_AJ24  657  --------------------------------------------------
T._trichiura_host_Nomascus_gab  704  GTCGCGAGCTGTCATCACGTCGCCGACCGCTCCCGTGGCGTTGATGCTGC
T._trichiura_host_Homo_sapiens  666  --------------------------------------------------
T._trichiura_host_Papio_ursinus 637  --------------------------------------------------
T._papionis_DGI                 609  --------------------------------------------------
T._papionis_DGII                600  --------------------------------------------------
T._papionis_DGIII               597  --------------------------------------------------
T._discolor_AB367795            794  --------------------------------------------------
T._discolor_AB367794            794  --------------------------------------------------
T._skrjabini_AJ489248           483  --------------------------------------------------
```

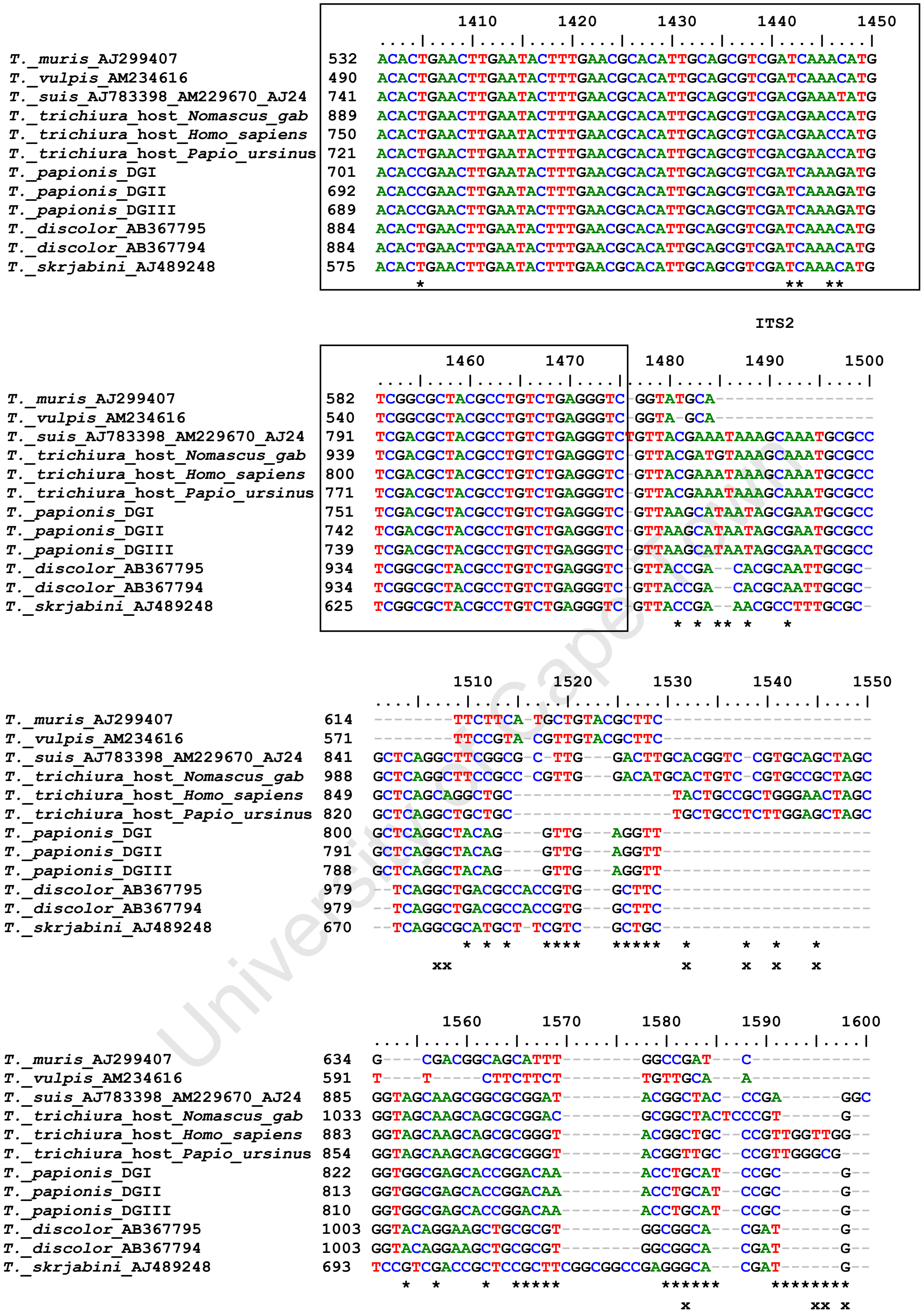
```
                                           1260      1270      1280      1290      1300
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               436  --------------------------------------------------
T._vulpis_AM234616              391  --------------------------------------------------
T._suis_AJ783398_AM229670_AJ24  657  --------------------------------------------------
T._trichiura_host_Nomascus_gab  754  GTCGTGCTATGTCGGTGAGGTGTAAAGAACGTCCGTTTGTCTCTTGAGCG
T._trichiura_host_Homo_sapiens  666  --------------------------------------------------
T._trichiura_host_Papio_ursinus 637  --------------------------------------------------
T._papionis_DGI                 609  --------------------------------------------------
T._papionis_DGII                600  --------------------------------------------------
T._papionis_DGIII               597  --------------------------------------------------
T._discolor_AB367795            794  --------------------------------------------------
T._discolor_AB367794            794  --------------------------------------------------
T._skrjabini_AJ489248           483  --------------------------------------------------
```

```
                                                                          5.8S rDNA

                                           1310      1320      1330      1340      1350
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               436  --TGACAAT--ATTCGAATG-CATTCCGAACGGCGGATCACTTGGCTCGT
T._vulpis_AM234616              391  --TGAAAAGAAAAAGGAACGACATTCCGAACGGCGGATCACTTGGCTCGT
T._suis_AJ783398_AM229670_AJ24  657  ----------ATGA-------CATTCCGAACGGCGGATCACTTGGCTCGT
T._trichiura_host_Nomascus_gab  804  CA--------ATGA-------CATTCCGAACGGCGGATCACTTGGCTCGT
T._trichiura_host_Homo_sapiens  666  ----------ATGA-------CATTCCGAACGGCGGATCACTTGGCTCGT
T._trichiura_host_Papio_ursinus 637  ----------ATGA-------CATTCCGAACGGCGGATCACTTGGCTCGT
T._papionis_DGI                 609  --CGCAGGAAAGTA-------CATTCCGAACGGTGGATCACTTGGCTCGT
T._papionis_DGII                600  --CGCAGGAAAGTA-------CATTCCGAACGGTGGATCACTTGGCTCGT
T._papionis_DGIII               597  --CGCAGGAAAGTA-------CATTCCGAACGGTGGATCACTTGGCTCGT
T._discolor_AB367795            794  --TGAATAGAGA---------CATTCCGAACGGCGGATCACTTGGCTCGT
T._discolor_AB367794            794  --TGAATAGAGA---------CATTCCGAACGGCGGATCACTTGGCTCGT
T._skrjabini_AJ489248           483  --TGAAAAGATATA-------CATTCCGAACGGCGGATCACTTGGCTCGT
                                       ******** **                    *
```

```
                                           1360      1370      1380      1390      1400
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               481  AGGTCGTTGAAGAACGACGTGACACTCGAGAATTGATGTGAATTGCAGAC
T._vulpis_AM234616              439  AGGTCGTTGAAGAACGACGTGACACTCGAGAATTGATGTGAATTGCAGAC
T._suis_AJ783398_AM229670_AJ24  690  AGATCGTTGAAGAACGACGTGACACTCGAGAATTGATGTGAATTGCAGAC
T._trichiura_host_Nomascus_gab  839  AGGTCGTTGAAGGACGACGTGACACTCGAGAATTGATGTGGATTGCAGAC
T._trichiura_host_Homo_sapiens  699  AGGTCGTTGAAGAACGACGTGACACTCGAGAATTGATGTGAATTGCAGAC
T._trichiura_host_Papio_ursinus 670  AGGTCGTTGAAGAACGACGTGACACTCGAGAATTGATGTGAATTGCAGAC
T._papionis_DGI                 650  AGATCGTTGAAGAACGACGTGACACTCGAGAATTGACGTGAATTGCAGAC
T._papionis_DGII                641  AGATCGTTGAAGAACGACGTGACACTCGAGAATTGACGTGAATTGCAGAC
T._papionis_DGIII               638  AGATCGTTGAAGAACGACGTGACACTCGAGAATTGACGTGAATTGCAGAC
T._discolor_AB367795            833  AGGTCGTTGAAGAACGACGTGACACTCGAGAATTGATGTGAATTGCAGAC
T._discolor_AB367794            833  AGGTCGTTGAAGAACGACGTGACACTCGAGAATTGATGTGAATTGCAGAC
T._skrjabini_AJ489248           524  AGGTCGTTGAAGAACGACGTGACACTCGAGAATTGATGTGAATTGCAGAC
                                       *                                 *
```

Figure 7.1 continued



```
                                            1410      1420      1430      1440      1450
                                      ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               532   ACACTGAACTTGAATACTTTGAACGCACATTGCAGCGTCGATCAAACATG
T._vulpis_AM234616              490   ACACTGAACTTGAATACTTTGAACGCACATTGCAGCGTCGATCAAACATG
T._suis_AJ783398_AM229670_AJ24  741   ACACTGAACTTGAATACTTTGAACGCACATTGCAGCGTCGACGAAATATG
T._trichiura_host_Nomascus_gab  889   ACACTGAACTTGAATACTTTGAACGCACATTGCAGCGTCGACGAACCATG
T._trichiura_host_Homo_sapiens  750   ACACTGAACTTGAATACTTTGAACGCACATTGCAGCGTCGACGAACCATG
T._trichiura_host_Papio_ursinus 721   ACACTGAACTTGAATACTTTGAACGCACATTGCAGCGTCGACGAACCATG
T._papionis_DGI                 701   ACACCGAACTTGAATACTTTGAACGCACATTGCAGCGTCGATCAAAGATG
T._papionis_DGII                692   ACACCGAACTTGAATACTTTGAACGCACATTGCAGCGTCGATCAAAGATG
T._papionis_DGIII               689   ACACCGAACTTGAATACTTTGAACGCACATTGCAGCGTCGATCAAAGATG
T._discolor_AB367795            884   ACACTGAACTTGAATACTTTGAACGCACATTGCAGCGTCGATCAAACATG
T._discolor_AB367794            884   ACACTGAACTTGAATACTTTGAACGCACATTGCAGCGTCGATCAAACATG
T._skrjabini_AJ489248           575   ACACTGAACTTGAATACTTTGAACGCACATTGCAGCGTCGATCAAACATG
                                          *                                    **  **

                                                                            ITS2

                                            1460      1470      1480      1490      1500
                                      ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               582   TCGGCGCTACGCCTGTCTGAGGGTC-GGTATGCA----------------
T._vulpis_AM234616              540   TCGGCGCTACGCCTGTCTGAGGGTC-GGTA-GCA----------------
T._suis_AJ783398_AM229670_AJ24  791   TCGACGCTACGCCTGTCTGAGGGTCTGTTACGAAATAAAGCAAATGCGCC
T._trichiura_host_Nomascus_gab  939   TCGACGCTACGCCTGTCTGAGGGTC-GTTACGATGTAAAGCAAATGCGCC
T._trichiura_host_Homo_sapiens  800   TCGACGCTACGCCTGTCTGAGGGTC-GTTACGAAATAAAGCAAATGCGCC
T._trichiura_host_Papio_ursinus 771   TCGACGCTACGCCTGTCTGAGGGTC-GTTACGAAATAAAGCAAATGCGCC
T._papionis_DGI                 751   TCGACGCTACGCCTGTCTGAGGGTC-GTTAAGCATAATAGCGAATGCGCC
T._papionis_DGII                742   TCGACGCTACGCCTGTCTGAGGGTC-GTTAAGCATAATAGCGAATGCGCC
T._papionis_DGIII               739   TCGACGCTACGCCTGTCTGAGGGTC-GTTAAGCATAATAGCGAATGCGCC
T._discolor_AB367795            934   TCGGCGCTACGCCTGTCTGAGGGTC-GTTACCGA--CACGCAATTGCGC-
T._discolor_AB367794            934   TCGGCGCTACGCCTGTCTGAGGGTC-GTTACCGA--CACGCAATTGCGC-
T._skrjabini_AJ489248           625   TCGGCGCTACGCCTGTCTGAGGGTC-GTTACCGA--AACGCCTTTGCGC-
                                                                    * * ** *   *

                                            1510      1520      1530      1540      1550
                                      ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               614   --------TTCTTCA-TGCTGTACGCTTC---------------------
T._vulpis_AM234616              571   --------TTCCGTA-CGTTGTACGCTTC---------------------
T._suis_AJ783398_AM229670_AJ24  841   GCTCAGGCTTCGGCG-C-TTG---GACTTGCACGGTC-CGTGCAGCTAGC
T._trichiura_host_Nomascus_gab  988   GCTCAGGCTTCCGCC-CGTTG---GACATGCACTGTC-CGTGCCGCTAGC
T._trichiura_host_Homo_sapiens  849   GCTCAGCAGGCTGC----------------TACTGCCGCTGGGAACTAGC
T._trichiura_host_Papio_ursinus 820   GCTCAGGCTGCTGC----------------TGCTGCCTCTTGGAGCTAGC
T._papionis_DGI                 800   GCTCAGGCTACAG----GTTG---AGGTT---------------------
T._papionis_DGII                791   GCTCAGGCTACAG----GTTG---AGGTT---------------------
T._papionis_DGIII               788   GCTCAGGCTACAG----GTTG---AGGTT---------------------
T._discolor_AB367795            979   --TCAGGCTGACGCCACCGTG---GCTTC---------------------
T._discolor_AB367794            979   --TCAGGCTGACGCCACCGTG---GCTTC---------------------
T._skrjabini_AJ489248           670   --TCAGGCGCATGCT-TCGTC---GCTGC---------------------
                                               * * *   ****   *****  *     *  *   *
                                            xx                       x     x  x   x

                                            1560      1570      1580      1590      1600
                                      ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               634   G----CGACGGCAGCATTT--------GGCCGAT---C------------
T._vulpis_AM234616              591   T----T-----CTTCTTCT--------TGTTGCA---A------------
T._suis_AJ783398_AM229670_AJ24  885   GGTAGCAAGCGGCGCGGAT--------ACGGCTAC--CCGA------GGC
T._trichiura_host_Nomascus_gab  1033  GGTAGCAAGCAGCGCGGAC--------GCGGCTACTCCCGT------G--
T._trichiura_host_Homo_sapiens  883   GGTAGCAAGCAGCGCGGGT--------ACGGCTGC--CCGTTGGTTGG--
T._trichiura_host_Papio_ursinus 854   GGTAGCAAGCAGCGCGGGT--------ACGGTTGC--CCGTTGGGCG---
T._papionis_DGI                 822   GGTGGCGAGCACCGGACAA--------ACCTGCAT--CCGC------G--
T._papionis_DGII                813   GGTGGCGAGCACCGGACAA--------ACCTGCAT--CCGC------G--
T._papionis_DGIII               810   GGTGGCGAGCACCGGACAA--------ACCTGCAT--CCGC------G--
T._discolor_AB367795            1003  GGTACAGGAAGCTGCGCGT--------GGCGGCA---CGAT------G--
T._discolor_AB367794            1003  GGTACAGGAAGCTGCGCGT--------GGCGGCA---CGAT------G--
T._skrjabini_AJ489248           693   TCCGTCGACCGCTCCGCTTCGGCGGCCGAGGGCA---CGAT------G--
                                         *  *    *  *****          ******     ********
                                                                     x            xx x
```

Figure 7.1 continued

```
                                             1610      1620      1630      1640      1650
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               657  ----GGCGAAC---GTTGCGCCGCTGCT-------------------T--
T._vulpis_AM234616              609  ----TGGAAGCTGTGCTGTGCGGCTGCT-------------------T--
T._suis_AJ783398_AM229670_AJ24  919  TGTGAGCGAGC---GCGACGCCGAGGCTCCT--CC---------TGCT--
T._trichiura_host_Nomascus_gab  1067 TCTGAGCGAGC---GCGACGCCGCAGGTCGT--CC---------TGCT--
T._trichiura_host_Homo_sapiens  921  TCTCAGCGAGC---GCGACGCCGCAGCTG-----CTCCTGCTGCTACT--
T._trichiura_host_Papio_ursinus 890  -CTGAGCGAGC---GCGACGCCGCAGCTG-----C---------TGCT--
T._papionis_DGI                 854  CGCGAGCGAGC---GTGACGCCGCAGCTCC---------------GTT--
T._papionis_DGII                845  CGCGAGCGAGC---GTGACGCCGCAGCTCC---------------GTT--
T._papionis_DGIII               842  CGCGAGCGAGC---GTGACGCCGCAGCTCC---------------GTT--
T._discolor_AB367795            1035 CGCCTCTGAGC---GTTACGCTGCTGCTGATGGCG---------GTCGAG
T._discolor_AB367794            1035 CGCCTCTGAGC---GTTACGCTGCTGCTGATGGCG---------GTCGAG
T._skrjabini_AJ489248           733  CGCCTGCGAGC---GCTGCGCCACTGGACATGGCG---------TGCG--
                                     ***            *            **    *         * *
                                     x  x                               xxxxxxxxx x


                                            1660      1670      1680      1690      1700
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               679  -GCCAAC----------------------------------GCAGCAGC-
T._vulpis_AM234616              634  -GCCATC----------------------------------G--GCGGC-
T._suis_AJ783398_AM229670_AJ24  953  -AGCAGCGA----CGGCAGGTGCCC-GTCATCGCTGGC-AGGCAGCCGG-
T._trichiura_host_Nomascus_gab  1101 -GGCAGCGA----CGGCAGGTGTTC-GCTATCGCTGCC-AGGCAGACGG-
T._trichiura_host_Homo_sapiens  961  -GGCAGCGA----CGGCAGGTGGCC-GTCATCGCTGAC-AGGCAGCCGC-
T._trichiura_host_Papio_ursinus 920  -GGCAGCGA----CGGCAGGTGGCC-GTCATCGCTGAC-AGGCAGCCGG-
T._papionis_DGI                 884  -GCCAGCGA-------------GCC-GCGATGGC-AAC-TGGTAGGCGG-
T._papionis_DGII                875  -GCCAGCGA-------------GCC-GCGATGGC-AAC-TGGTAGGCGG-
T._papionis_DGIII               872  -GCCAGCGA-------------GCC-GCGATGGC-AAC-TGGTAGGCGG-
T._discolor_AB367795            1073 TGCCGCTGG-------------GCCAGCCGCAGCTGGC-CGGCAACCGC-
T._discolor_AB367794            1073 TGCCGCTGG-------------GCCAGCCGCAGCTGGC-CGGCAACCGC-
T._skrjabini_AJ489248           769  -GTCGTTGGCCCT---------GTCGGCCCCAGCCGACGCGGCAACCGAT
                                       *          *********     **  *  **   *  *  *
                                                                                x


                                             1710      1720      1730      1740      1750
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               693  ---------------AGCA---GCGGA-CGGAGCTTGCTCGACAAAGGTG
T._vulpis_AM234616              646  ---------------GGCA---GCCGAGCGGAGCTAGCTCGGCAAAGGAG
T._suis_AJ783398_AM229670_AJ24  994  ---------------AGCT---GCGGAGAGCGGCTAACTCAGCGCAGTAC
T._trichiura_host_Nomascus_gab  1142 ---------------ACCA---GCGGAGAGCGGCTAACTCAGCGCAGCAC
T._trichiura_host_Homo_sapiens  1002 ---------------AGCTTCTGCGGAGAGCGGCTAACTCAGCGCAGTAC
T._trichiura_host_Papio_ursinus 962  ---------------AGCT---GCGGAGAGCGGCCAACTCAGCGCAGTAC
T._papionis_DGI                 915  ---------------AGCA---GCGGAGAGCGGCCAAGTCAGCGTAGGGC
T._papionis_DGII                906  ---------------AGCA---GCGGAGAGCGGCCAAGTCAGCGTAGGGC
T._papionis_DGIII               903  ---------------AGCA---GCGGAGAGCGGCCAAGTCAGCGTAGGGC
T._discolor_AB367795            1107 -----------TACTAGCA---GCAGAGAGCAGTCGGCTCGGCGGAGAAC
T._discolor_AB367794            1107 -----------TACTAGCA---GCAGAGAGCAGTCGGCTCGGCGGAGAAC
T._skrjabini_AJ489248           809  CGCCGCTGCCGTGTTCGCA---GTGGAGAGCAGTCGGCTCGGCGAAGAAC
                                                       *                  *      *  **
                                                        xxx            x


                                            1760      1770      1780      1790      1800
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               724  CTTAGCTTTGTCCGAGCATGTTCGAT---CGCAA------GGTGCC-TCA
T._vulpis_AM234616              678  GTTAGCTTTCTCCGAGCATGCTCGACGAAAGCAA------GGTGCC-TCG
T._suis_AJ783398_AM229670_AJ24  1026 GGAAGCTG--CCCGAGTTGGCTACGT---CGTCGCTACATCGT-CG-TCA
T._trichiura_host_Nomascus_gab  1174 GGAAGCTG--CCCGAGTCGGCTACGT---CGCCG------CGT-CG-TCG
T._trichiura_host_Homo_sapiens  1037 GGAAGCTG--CCCGAGTTGGCTATGT---CGCTA------CAT-CG-TCA
T._trichiura_host_Papio_ursinus 994  GGAAGCTG--CCCGAGTTGGCTATGT---CGCTA------CAT-CG-TCA
T._papionis_DGI                 947  GAAGACTA--CCCGACTTGGCTAC-C---GGCCG------CGC-CG-TCG
T._papionis_DGII                938  GAAGACTA--CCCGACTTGGCTAC-C---GGCCG------CGC-CG-TCG
T._papionis_DGIII               935  GAAGACTA--CCCGACTTGGCTAC-C---GGCCG------CGC-CG-TCG
T._discolor_AB367795            1143 GTAGGCCT--TCCGAGTCGACT---T---TTCAT------GCT-CG-TAA
T._discolor_AB367794            1143 GTAGGCCT--TCCGAGTCGACT---T---TTCAT------GCT-CG-TAA
T._skrjabini_AJ489248           856  GTAGGCTT--CCCGAGTCGGCT---T---GACGA------TCT-CGATCA
                                      * **  *       *       ***   *  **       **      *
```

Figure 7.1 continued

```
                                              1810      1820      1830      1840      1850
                                      ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               765   GCAGC---------------CAAC--------------------------
T._vulpis_AM234616              722   GCGGCGGCGGCAGTCGATCTCCGG--------------------------
T._suis_AJ783398_AM229670_AJ24  1070  GCGTA---------------CAGC--GCGACTGA--GTTGTTTTCACCAC
T._trichiura_host_Nomascus_gab  1212  GCG------------------------CGACCGTCCGTTG-----ACCAC
T._trichiura_host_Homo_sapiens  1075  GCGTA---------------AAGCCGGCGAACGACCGTTG-----ACCAC
T._trichiura_host_Papio_ursinus 1032  GCGTA---------------AAGCGCGCGACCGACCGTTG-----ACCAC
T._papionis_DGI                 984   GCGTA---------------CAGC---------A--GTTG-----AGCAG
T._papionis_DGII                975   GCGTA---------------CAGC---------A--GTTG-----AGCAG
T._papionis_DGIII               972   GCGTA---------------CAGC---------A--GTTG-----AGCAG
T._discolor_AB367795            1178  TCG-----------------------------------------------
T._discolor_AB367794            1178  TCG-----------------------------------------------
T._skrjabini_AJ489248           891   TCGTC---------------TAGT--------------------------
                                                          *   ********* **          *  *
                                                              xx    x
```

```
                                              1860      1870      1880      1890      1900
                                      ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               774   -----------------------CATC---ACGCGTCGGTGG--------
T._vulpis_AM234616              746   -----------------------CAGC---AGCCGGCGATGT--------
T._suis_AJ783398_AM229670_AJ24  1101  CGAGCGACCACCCCGCGCGCGCG-ACC-GTAGTCGTCCGTCTTCGTCAC-
T._trichiura_host_Nomascus_gab  1233  CGAGCGACCA--TCGCAAT--CG-AGC-GCAGTCGTCCGTCCTCGTTGC-
T._trichiura_host_Homo_sapiens  1105  CGAGCGACCA--CTGCGGGCGCG-AGC-GCAGTCGTCCGTCTTCGTCGC-
T._trichiura_host_Papio_ursinus 1062  CGAGCAACCA--TCGCGTGCGCG-AGC-GCAGTCGTCCGTCTTCGTCGC-
T._papionis_DGI                 1003  GGAGCGGTGACCGCACGCGCTCGTAGCAGCAAGTGTTCGTCGTAGTTGCA
T._papionis_DGII                994   GGAGCGGTGACCGCACGCGCTCGTAGCAGCAAGTGTTCGTCGTAGTTGCA
T._papionis_DGIII               991   GGAGCGGTGACCGCACGCGCTCGTAGCAGCAAGTGTTCGTCGTAGTTGCA
T._discolor_AB367795            1181  -----------------------CGGC-GCAGGCGACCATCG--------
T._discolor_AB367794            1181  -----------------------CGGC-GCAGGCGACCATCG--------
T._skrjabini_AJ489248           900   -----------------------CAGC-GCAGGCGACCATCG--------
                                      *    **** *** *  *  *  *   *   ***  *    * *  *  *
                                           x      xx   x
```

```
                                              1910      1920      1930      1940      1950
                                      ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               789   --------TGGTTGAGCGGGCT-GCTGTCGTGG-----------------
T._vulpis_AM234616              761   --------TGATCGGATCGGCTGGCCGCCCGCC-----------------
T._suis_AJ783398_AM229670_AJ24  1148  CGGCCCCTAGATCGA--CGGCA-GCAGCAGTCGACTAGTAGACGACGACG
T._trichiura_host_Nomascus_gab  1276  CGCTCCCTAGATCGA--CGGCA-GTGGCAGTCGACTAGTAGACGACGACG
T._trichiura_host_Homo_sapiens  1150  CGCCCCCTAGATCGA--CGGCA-GCGGCAGTCGACTAGAGGACGACGACG
T._trichiura_host_Papio_ursinus 1107  CGCCCCCTAGATCGA--CGGCA-GCGGCAGTCGACTAGAAGACGACGACG
T._papionis_DGI                 1053  CGGCAGCAGCAGCAG--CGGCA-GCAGCAGTCGAC-----GACGACGACG
T._papionis_DGII                1044  CGGCAGCAGCAGCAG--CGGCA-GCAGCAGTCGAC-----GACGACGACG
T._papionis_DGIII               1041  CGGCAGCAGCAGCAG--CGGCA-GCAGCAGTCGAC-----GACGACGACG
T._discolor_AB367795            1198  --------AGA--AA--CGGCT-GCAA-AGTCGTC-----GGCATCGA--
T._discolor_AB367794            1198  --------AGA--AA--CGGCT-GCAA-AGTCGTC-----GGCATCGA--
T._skrjabini_AJ489248           917   --------AGATGAA--CGACT-GCAA-----------------------
                                        * ** *** * **          *         *****
                                                                              x
```

```
                                              1960      1970      1980      1990      2000
                                      ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               813   -CAAT-GCCGAACG---GGTCTGAC--CGGTTGGATGCAA-GATTGAACC
T._vulpis_AM234616              786   -CGCT-ACC--ACC---GTCCTGGCGGCGGCGCCACCGAACGACCGCCGC
T._suis_AJ783398_AM229670_AJ24  1195  ------GCT--GCT---ACGCGCTGCGCGGCGG----------TCG--T-
T._trichiura_host_Nomascus_gab  1323  ACGGCTGCT--GCTGCTACGCGATCCGCGGCGGC----------------
T._trichiura_host_Homo_sapiens  1197  GCGTCTGCT--GCT---ACGCGCTCTGCAGCGGC-------GATCT--C-
T._trichiura_host_Papio_ursinus 1154  GCGTCTGCT--GCT---ACGCGCTCTGCGGCGGC-GGCAGCGATCT--C-
T._papionis_DGI                 1095  ACGAA-ACC--GTT---CGCCTTGCTGCGGCGGCGGGCACCGCTCGACC-
T._papionis_DGII                1086  ACGAA-ACC--GTT---CGCCTTGCTGCGGCGGCGGGCACCGCTCGACC-
T._papionis_DGIII               1083  ---AA-ACC--GTT---CGCCTTGCTGCGGCGGCGGGCACCGCTCGACC-
T._discolor_AB367795            1227  --------------------------------------AACAGTCGACT-
T._discolor_AB367794            1127  --------------------------------------AACAGTCGACT-
T._skrjabini_AJ489248           933   --------------------------------------------------
                                      *  **** *   *    *** ***          *    *  *  ***
                                      +++                         x      xxxxxx
```

Figure 7.1 continued

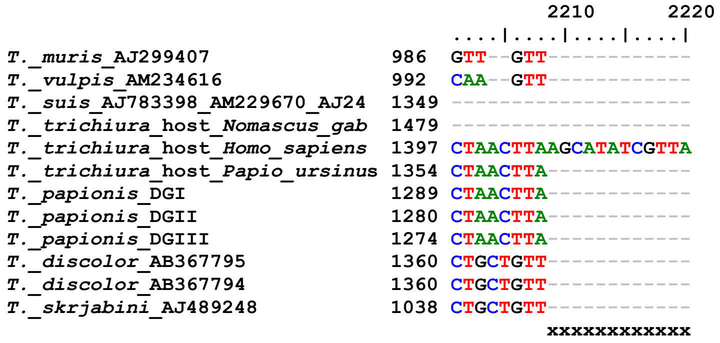
```
                                            2010      2020      2030      2040      2050
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               856  GGT--CGGCC---GGGGCAGACGTTGC---ACAC-AATGGTCT---T---
T._vulpis_AM234616              830  GGTCGCGGTC---GCGGCAGACGTTGC---AGCC-AATGGTTC---T---
T._suis_AJ783398_AM229670_AJ24  1220 -GG--CTGCGCCGGCGGCAAACGTTGC-TGACAC-TCCGCTAC---TACC
T._trichiura_host_Nomascus_gab  1354 ---------------GGCAAACGTTGC-TGACAC-ACCGCTAC---TACC
T._trichiura_host_Homo_sapiens  1231 -GG--CTGCG---ACGGCAAACGTTGC-TGACAC-ACCGCTGC---TACC
T._trichiura_host_Papio_ursinus 1194 -GG--CTGCG---ACGGCAAACGTTGC-TGACAC-ACCGTTAC---TACC
T._papionis_DGI                 1137 -GA--CGACG---GCGGCAAACGTTGC-TGACAC-ACTGCTACCGGTCAG
T._papionis_DGII                1128 -GA--CGACG---GCGGCAAACGTTGC-TGACAC-ACTGCTACCGGTCAG
T._papionis_DGIII               1122 -GA--CGACG---GCGGCAAACGTTGC-TGACAC-ACTGCTACCGGTCAG
T._discolor_AB367795            1238 -TT--CAGTC---GCGGCAAGCGTTGATTGAGGC-AGTAC-GC---GCAG
T._discolor_AB367794            1238 -TT--CAGTC---GCGGCAAGCGTTGATTGAGGC-AGTAC-GC---GCAG
T._skrjabini_AJ489248           933  ------AGTC---GCGGCAAGCGTTGCGTTACACGAATGC-AC---GCGG
                                       *   **     *                       * *   *** ***
                                                                           x x


                                            2060      2070      2080      2090      2100
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               891  ------------TGCCA------G---CGGCCGGCGTC-----AGTCCGT
T._vulpis_AM234616              867  ------------TGCCA------GCAACGGCCGGCGACTTGGCAGCCGGT
T._suis_AJ783398_AM229670_AJ24  1262 ---AC---ATGCTGCTG------GTAGCGGC-GGCGTCTTTGCCGTACAG
T._trichiura_host_Nomascus_gab  1384 ---GCTTGCTGCTGCTG------GTAGCGGC-GGCGTCTTTGCCGTACGC
T._trichiura_host_Homo_sapiens  1270 ---ACTTGCTGCTGCTGCTGCTGGTAGCGGC-GGCGTCTTTGCCGTACGC
T._trichiura_host_Papio_ursinus 1233 ---ACTTGTTGCTGCTG------GTAGCAGC-GGCGTCTTTGCCGTACGC
T._papionis_DGI                 1179 ---GC---GAGCTGCCG------GTAGC----GGCGTCTTTGCCGTTCG-
T._papionis_DGII                1170 ---GC---GAGCTGCCG------GTAGC----GGCGTCTTTGCCGTTCG-
T._papionis_DGIII               1164 ---GC---GAGCTGCCG------GTAGC----GGCGTCTTTGCCGTTCG-
T._discolor_AB367795            1277 ---GC---GTCCTG----------------------TCCTTGCCG-----
T._discolor_AB367794            1277 ---GC---GTCCTG----------------------TCCTTGCCG-----
T._skrjabini_AJ489248           970  CTAGC---GTGCTG----------------------TC-TTGCCG-----
                                        * *****     *            ***               *  *
                                             x        xxxxxx     x


                                            2110      2120      2130      2140      2150
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               915  TGCGC-----TAATGCCGGCTGCTCGGCGGT-TGCCAACG------ACAT
T._vulpis_AM234616              899  TGAGCGCCAGCAGTGCCGGCCGATCGGAGGT-TGCCAACGG----GACGT
T._suis_AJ783398_AM229670_AJ24  1300 TG-GT-----GACTCTCAGCCGC----CGCA-ACG--AGTGCGCTCCCGT
T._trichiura_host_Nomascus_gab  1425 TG-GT-----CACTCTCGGCCGC----CGCA-AAGCGACTGCGCTCCCGT
T._trichiura_host_Homo_sapiens  1317 TG-GT-----CAGTCACGGCCGC-------A-ACGCCACTGCGCTCCCGT
T._trichiura_host_Papio_ursinus 1274 TG-GT-----CACCGTCGGCCGC-------T-ACGCCACTGCGCTCTCGT
T._papionis_DGI                 1212 ---------------TCAACTAG----CGGT-TCGCCGCGTGGCTCCACC
T._papionis_DGII                1203 ---------------TCAACTAG----CGGT-TCGCCGCGTGGCTCCACC
T._papionis_DGIII               1197 ---------------TCAACTAG----CGGT-TCGCCGCGTGGCTCCACC
T._discolor_AB367795            1294 ------------------GCTGC----CCGTTTGGCTGCTG----CTCGG
T._discolor_AB367794            1294 ------------------GCTGC----CCGTTTGGCTGCTG----CTCGG
T._skrjabini_AJ489248           989  ------------------GCTGC----CCGT-TGGCTGCTG----CTCGT
                                     ** **     *****  ** ***    ***  *    * ***    ****
                                                 xxxx              x               x


                                            2160      2170      2180      2190      2200
                                     ....|....|....|....|....|....|....|....|....|....|
T._muris_AJ299407               953  GAATGGACGAGCG-C----------------CTAAATTGTGCGCAGTCGC
T._vulpis_AM234616              944  AGAGGCACGCTCG-CGCGC-GCTTAGCTTAGCTTAGCTTAGCGCGGCAGC
T._suis_AJ783398_AM229670_AJ24  1337 ---TGT-TGT-----TCG-TGTT---------------------------
T._trichiura_host_Nomascus_gab  1464 ---TCT-TGT-TG-TTCG-TGTT---------------------------
T._trichiura_host_Homo_sapiens  1353 ---TGT-TGTCTC-TTCG-TGTTGACCTCAGATCAGACGAGGCTACCCGC
T._trichiura_host_Papio_ursinus 1310 ---TGT-TGTGTC-TTCG-TGTTGACCTCAGATCAGACGAGGCTACCCGC
T._papionis_DGI                 1242 ---CGTACGTCTC-CTCGATGTTGACCTCAGATCAGACGAGGCTACCCGC
T._papionis_DGII                1233 ---CGTACGTCTC-CTCGATGTTGACCTCAGATCAGACGAGGCTACCCGC
T._papionis_DGIII               1227 ---CGTACGTCTC-CTCGATGTTGACCTCAGATCAGACGAGGCTACCCGC
T._discolor_AB367795            1318 ---TGGAAGCTAGTTGCGCTGGT--CCGCAGA----ACGAGTGGTCGCTT
T._discolor_AB367794            1318 ---TGGAAGCTAGTTGCGCTGGT--CCGCAGA----ACGAGTGGTCGCTT
T._skrjabini_AJ489248           1012 ---TGGTAGTTTA-TGCGCTGCT--CCG-------------------CTT
                                        *  **  *   *   *
                                               x
```

Figure 7.1 continued



```
                                             2210      2220
                                         ....|....|....|....|
T._muris_AJ299407                    986  GTT--GTT------------
T._vulpis_AM234616                   992  CAA--GTT------------
T._suis_AJ783398_AM229670_AJ24      1349  --------------------
T._trichiura_host_Nomascus_gab      1479  --------------------
T._trichiura_host_Homo_sapiens      1397  CTAACTTAAGCATATCGTTA
T._trichiura_host_Papio_ursinus     1354  CTAACTTA------------
T._papionis_DGI                     1289  CTAACTTA------------
T._papionis_DGII                    1280  CTAACTTA------------
T._papionis_DGIII                   1274  CTAACTTA------------
T._discolor_AB367795                1360  CTGCTGTT------------
T._discolor_AB367794                1360  CTGCTGTT------------
T._skrjabini_AJ489248               1038  CTGCTGTT------------
                                                  xxxxxxxxxxxx
```

Figure 7.1 continued

A phylogenetic analysis was carried out with the ITS1-5.8S rDNA-ITS2 sequences of *Trichuris* isolated from Da Gama Park baboons, CP_GOB baboons, humans, and other *Trichuris* found in GenBank. The phylogenetic comparison revealed that the *Trichuris* isolated from Da Gama Park baboon hosts (DGI, DGII, and DGIII) was more distantly related to the human *T. trichiura* than to the *T. suis* isolated from pigs (Figure 7.2). Thus, it is likely that the *Trichuris* isolated from the Da Gama Park troop of baboons are a phylogenetically distinct species of *Trichuris* and were named *Trichuris papionis.*

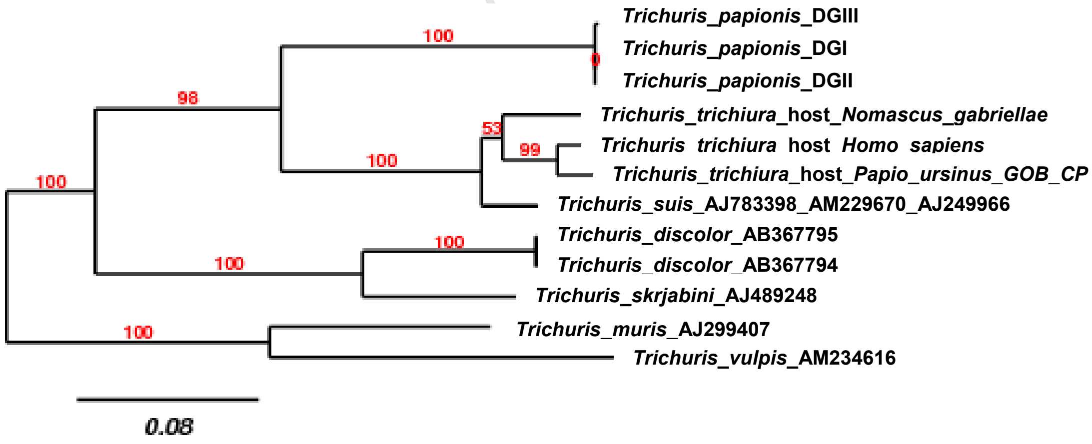


Figure 7.2 Phylogram of different species of the genus *Trichuris*, *T. papionis* from baboon hosts and *T. trichiura* from human and baboon hosts, constructed with PhyML, and based on the PRANK alignment of ITS1-5.8S rDNA-ITS2 sequences. Percentage values from the approximate likelihood ratio test are indicated at nodes. The scale bar shows the numbers of substitutions per site.

The phylogenetic analysis also showed that the *Trichuris* isolated from baboons ranging in the CP and GOB troops was more closely related to *T. trichiura* isolated from human hosts from

Cameroon (Figures 7.1, 7.2) and *T. trichiura* isolated from monkeys kept in a Spanish zoo, than to *Trichuris papionis* isolated from Da Gama Park baboons. There was high similarity between *Trichuris* isolated from CP_GOB baboons and *T. trichiura* isolated from humans (91% similarity between ITS1-5.8S rDNA-ITS2 sequences). By contrast, *Trichuris* isolated from CP_GOB baboons and *Trichuris papionis* isolated from Da Gama Park baboons were much less similar (58% similarity; see differences in Figure 7.1). The *Trichuris* isolated from the CP and GOB troops was therefore named *T._trichiura*_host_*Papio_ursinus*_GOB_CP, based on the phylogenetic analysis. ITS1-5.8S rDNA-ITS2 sequences from *T. papionis* (DGI, DGII, and DGIII), *T. trichiura* and *T._trichiura*_host_*Papio_ursinus*_GOB_CP are deposited in GenBank under accession nos.: GQ301553 (*T. papionis* DGI), GQ301552 (*T. papionis* DGII), GQ301551 (*T. papionis* DGIII), GQ301555 (*T. trichiura*), and GQ301554 (*T._trichiura*_host_*Papio_ursinus*).

CHAPTER EIGHT

DISCUSSION

8.1 Parasite infections in the Cape Peninsula baboons

In this study, I provide the first data on the gastrointestinal parasite species diversity and degree of infection for six troops of the Cape Peninsula baboon population. Seven helminth taxa, all nematodes, and eight protozoa were detected. All the helminth taxa found are classified as parasites causing varying degrees of clinical symptoms (Appendix D), while only two of the eight protozoa species found (*Balantidium coli* and *Entamoeba histolytica*) are known to be pathogenic to nonhuman primates; the other protozoa species found, including *E. coli* and *E. dispar*, are considered to be commensals of nonhuman primates (Cogswell 2007).

8.1.1 Variation in parasite infections throughout South Africa and Africa

The helminth diversity found in the Cape Peninsula baboon population (seven helminth taxa) is similar to what has been found in other South African localities. Higher helminth diversity (12 taxa) was reported by Appleton *et al.* (1991) in Mkuzi Game Reserve and was attributed to the high humidity associated with the subtropical climate and consequently favourable conditions for the development of infective stages of parasites. By contrast, the low helminth diversity (three taxa) found in chacma baboons in Namibia by Appleton and Brain (1995) was explained by the hot and dry climatic conditions, which are not ideal for the survival of infectious stages of helminths. These marked regional differences demonstrate the importance of environmental conditions on the viability and behaviour of parasite propagules, as suggested by Rogers and Sommerville (1963).

The most common helminth found in chacma baboons appeared to be the nematode *Physaloptera* sp., which has been found in all chacma baboon populations studied to date (Myers *et al.* 1971; Goldsmid 1974; McConnell *et al.* 1974; Goldsmid & Rogers 1978; Pettifer 1984; Appleton *et al.* 1986; Appleton *et al.* 1991), except for Namibia (Appleton &

Brain 1995). This nematode is transmitted indirectly to the baboon through intermediate hosts such as beetles, cockroaches, and other insects (Brack 1987). Another nematode with an indirect life cycle, *Streptopharagus* sp. (transmitted through arthropods), has been found in all populations of chacma baboon, including Pringle Bay (this study), but not in the Cape Peninsula or Wildcliff Nature Reserve. Eggs of another unidentified spirurid nematode were found at very low prevalence in the Cape Peninsula. Other nematodes found frequently across South Africa were *Oesophagostomum* sp. and *Trichostrongylus* sp. (both found in 12 of the 14 localities mentioned), and *Trichuris* sp. (present in 10 out of 14 localities). *Ternidens deminutus* eggs were absent from faecal samples from the Cape Peninsula, Pringle Bay, and Wildcliff areas and no adult specimens were recovered from the five necropsies performed on baboons of the Cape Peninsula. The absence of *Enterobius* sp. could be due to the fact that the eggs are rarely found in faeces, adhering instead to the peri-anal skin, which was not sampled in this study. *Strongyloides fuelleborni* was not found in the Cape Peninsula, Pringle Bay, or Wildcliff baboon faecal samples. Premvati (1958a,b,c) found that larvae of this species do not develop at temperatures below 15°C and it is thus possible that low winter temperatures in the Western Cape (the region encompassing all study sites) may have precluded this species from this region.

The presence of the nematode *Ascaris* sp. in the Cape Peninsula population is the first record of this parasite in southern African baboons. *Ascaris* sp. has been reported in only four other studies on baboon parasites, including three studies on olive baboons (*Papio anubis*), one in Kenya (Eley *et al.* 1989) and two in Uganda (Ocaido *et al.* 2003; Hope *et al.* 2004), and one study on hamadryas baboon (*Papio hamadryas*), in Saudi Arabia (Nasher 1988). In all of the above cases, a certain degree of interaction with humans was suggested to underpin the presence of this parasite in baboons. The high human density in the Cape Peninsula in addition to the medium prevalence (25%) of *Ascaris* eggs in human faeces (Adams *et al.* 2005) would suggest a similar causal link between humans and the presence of *Ascaris* in baboons of the Cape Peninsula.

No cestodes were found in any of the locations sampled in the present study. In particular, the absence of *Bertiella studeri* is striking since this cestode, indirectly transmitted through oribatid mites, has been found in all other baboon parasite studies in South Africa. The absence of the trematode *Schistosoma* sp. is readily explained by the complete absence of the obligate intermediate host (viz., snails of the genus *Biomphalaria*).

In summary, helminth diversity seems to be similar in baboon populations across South Africa. The diversity of intestinal protozoa was also very similar across South Africa with *Balantidium coli*, *Entamoeba coli*, and *Iodamoeba butschlii* being present in every locality investigated. Interestingly, the flagellate protozoan *Giardia* sp. in chacma baboon has only been reported to date in Namibia (Appleton & Brain 1995) but not in South Africa.

While the diversity of intestinal helminths and protozoa were similar in different populations in South Africa, prevalence was more variable. A similar pattern was found by Gillespie *et al.* (2004) when comparing parasite diversity and prevalence in blue monkeys (*Cercopithecus mitis*) from different localities. Prevalences calculated for helminths in the present study were typically similar to or lower than prevalences recorded in other South African study sites. Thus, prevalences of *Trichuris* sp. and *Oesophagostomum* sp. were similar to prevalences found in Pringle Bay, Wildcliff, and Giant's Castle (Appendix A) while prevalences of *Trichostrongylus* sp. and *Physaloptera* sp. were lower than in the majority of the other studies. Helminth taxa prevalences in the Cape Peninsula baboons (with the exception of *Trichuris* sp.) were most similar to those from Limpopo Province, situated in the northern part of the country, and significantly different from the two locations closest to the Cape Peninsula, namely Pringle Bay and Wildcliff. By contrast, prevalences of protozoa were more similar between the Cape Peninsula and Pringle Bay than to Wildcliff and Northern Transvaal and showed the highest prevalence for *B. coli* and one of the highest prevalences for *E. coli*. Climate has been proposed as an important factor explaining the variation of prevalences for one taxon among various sites (Nunn *et al.* 2005). Climatic conditions vary greatly among the localities compared in South Africa, from the coastal, subtropical climate of Mkuzi (Appleton & Henzi 1993) to the montane/subalpine climatic conditions found at Giant's Castle (Appleton *et al.* 1986) and the Mediterranean conditions of the Cape Peninsula. It is plausible that much of the variation in prevalences is a function of the impact of environmental factors on the survival of infective stages and hence on the rate of infection of baboons in the different localities.

The similarity of the gastrointestinal parasites among the various species of baboons in Africa suggests the presence and predominance of generalist parasites. In olive baboon, *Oesophagostomum* sp. and *Trichuris* sp. are commonly reported (Kuntz & Myers 1966; Kuntz & Myers 1967; Eley *et al.* 1989; McGrew *et al.* 1989; Müller-Graf *et al.* 1996; Munene *et al.* 1998; Murray *et al.* 2000; Hahn *et al.* 2003; Ocaido *et al.* 2003; Hope *et al.* 2004; Legesse &

Erko 2004), as in the chacma baboon. The presence of *Streptopharagus* sp. and *Strongyloides* sp. is also common in the olive baboon. Both helminths are found in *Papio ursinus* as well. Helminth diversity of yellow baboon (*Papio cynocephalus*) (Kuntz & Moore 1973; Meade 1984; Hahn *et al.* 2003), like that of olive baboon, shows low variation compared to the South African populations studied. For hamadryas baboon, helminth diversity is very similar among the different localities (all in Saudi Arabia; Nasher 1988; Ghandour *et al.* 1995) and mean diversity levels are very low compared to other species of baboons. It is likely that lower helminth diversity in hamadryas is a consequence of the high temperatures and low humidity typical of the Saudi Arabian study localities. Most protozoa reported across Africa are the same as those found in the present study, with the exception of *Giardia* sp. *Giardia* sp. appears to be very common in hamadryas baboon, less common in olive baboon, and found rarely or not at all in yellow and chacma baboon.

Parasite egg production is frequently used as a measure of infection intensity (e.g., Gulland 1992; Ezenwa 2003) and a few authors have found a positive correlation between individual egg output and worm biomass (Shaw & Moss 1989; Skorping *et al.* 1991). However, egg production has also been shown to be highly variable in the same host (Chapman *et al.* 2006b) and thus caution needs to be exercised when using this variable as an index of actual infection intensity. In the present study, it was not possible to compare egg output values to the host's worm biomass due to the non-invasive nature of faecal sampling.

The median egg output of nematodes in the Cape Peninsula was in the range of what has been defined by other authors (Stettler *et al.* 1998) as a low-intensity infection, corresponding to the classes of low-intensity helminth infection proposed by WHO (2002). Variation in egg output between parasite species of baboons from different localities in the region was substantial. The highest egg output for *Trichuris* sp. was found for samples collected from the Wildcliff troop (2317 eggs/g) with the Peninsula and Pringle Bay averaging only 74 and 33 eggs/g respectively. The high *Trichuris* sp. egg output in Wildcliff is associated with a very high prevalence of this worm (98%) and appeared to be both equally dispersed and at high loads in all samples. In general, *Trichuris* sp. egg output for these three Western Cape localities appears higher than other areas in South Africa (Appleton & Henzi 1993). A similar pattern emerged for *Trichostrongylus* sp. with both the Cape Peninsula and Wildcliff having low (6%) and medium (48%) prevalence and correspondingly low egg production.

Furthermore, in Pringle Bay, the high prevalence of this parasite (100%) corresponded to a high egg output (128 eggs/g).

Thus, there was a positive association between prevalence and egg output for a given species of helminth suggesting that, as reported in previous studies (e.g., Gulland 1992; Ezenwa 2003), high egg output translates into more infected individuals which in turn results in higher prevalence (i.e., it will not be confined to only a few, highly infected individuals). Finally, it is important to reiterate that the sexes are separate in nematodes and thus hosts infected with male worms only would not have eggs in their faeces and would therefore not test positive for a given parasite, even if they are infected with it. This could influence reports on parasite infection levels that are extrapolated from invasive versus non-invasive sampling techniques used on hosts.

8.1.2 Cumulative samples and sample- versus individual-calculated prevalence

For summer and winter data, a significant positive correlation was found between the number of cumulative samples analyzed per individual and the cumulative number of helminth and protozoa species detected. For summer data, cumulative species richness for individuals was not significant if the number of samples analyzed per individual was ≥ 3 samples, while for winter data there was a positive relationship between cumulative number of parasites detected and sample size up to and including five samples per individual. This difference between seasons might be due to the small number of faecal samples collected from the troops during the winter season. In general, therefore, my findings support those of Huffman *et al.* (1997) and Mühlenbein (2005), which both showed that the accuracy of assessing parasite prevalence of a group increased with an increase in the number of samples obtained per individual within each group. The minimum number of three sequential samples per individual obtained for the summer data corresponded to the minimum number reported by Mühlenbein (2005) (three to four samples). The minimum number extrapolated by Meade (1984) was however much higher, at ≥ 9. Together these results suggest that each study group requires independent evaluation of the minimum number of samples required to obtain a reliable estimate of parasite prevalence.

Parasite species richness (PSR) and prevalences calculated from faecal samples collected from known individuals were compared to the same indices of infection calculated from samples comprising a combination of known and unknown individuals (collectively treated as unknown). Both PSR and prevalence indices were significantly higher for samples calculated from known individuals when compared to the same indices calculated from the 'unknown' samples. This result is in agreement with those of Huffman *et al.* (1997) and Mühlenbein (2005), who both reported that using the number of samples as opposed to the number of individuals to calculate prevalence can bias the data (true prevalence from individuals being higher than infection rate from samples). Prevalence calculated from unknown samples could also be a concern since repeat samples are likely to occur and therefore a small number of animals with high infection levels and high PSR could be over-represented, particularly since sick animals could defecate more often than healthy ones (Mühlenbein 2005). This did not seem to be the case in the present study, where the opposite trend was apparent, namely, the majority of individuals analyzed harboured between two and four helminth taxa and between four and six protozoan taxa; thus, there did not seem to be few individuals with higher parasite diversity. It was for this reason that most of the findings discussed below are based on indices calculated from samples and not individuals. Thus, the emphasis of this thesis is on comparisons at both the troop and regional level rather than at the level of the individual. It is important to bear this in mind when comparing these results to those of other studies, some of which report true prevalences and others the percentage of samples found to be positive (Mühlenbein 2005).

8.1.3 Effects of season on parasite infection

The most limiting factor for survival of parasite infective stages (helminth eggs and protozoan cysts), and therefore for infection risk, is soil moisture (Rogers & Sommerville 1963). At any particular temperature, survival of infective stages is greatest when conditions are most humid. Furthermore, the survival of eggs at low humidities is greatest when temperatures are low. The Cape Peninsula climate is characterized by cold, wet winters (with a mean minimum daily temperature of 10.5°C during the study period and mean rainfall of ca. 351 mm) and hot, dry summers (with a mean maximum daily temperature of 23.5°C and mean rainfall of ca. 135 mm during the study period). Thus, indices of infection (PSR, prevalence, and egg output) were expected to be higher in the cooler winter season, when rainfall and ground humidity are also higher. Conversely, the hot, dry summer season was expected to have a negative impact on the survival of infective stages and hence lower PSR, prevalence, and egg output values were predicted.

Seasonal patterns varied according to the study troop and there was no overall effect of season evident for PSR, prevalence, or egg output across the study troops sampled in the Peninsula. Buffels Bay troop did not reveal any seasonality in any of the indices of infection analyzed. The same parasite taxa were found in both summer and winter seasons. Similarly, no seasonal pattern was evident in parasite diversity in the Plateau Road troop, with helminth diversity being similar in summer and winter. There was however a significant difference between the two winter seasons analyzed: helminth diversity was significantly lower in winter 2007 compared to winter 2006. Minimum and maximum temperatures where similar between these two seasons, but total rainfall in winter 2007 (435 mm) was almost the double than total rainfall (267 mm) in winter 2006, suggesting a potential negative effect of humidity on helminth infection, contrary to predictions. Protozoan species diversity was significantly affected by season, although the difference was contrary to the prediction with winter protozoan diversity being lower than the preceding summer protozoan diversity. Similarly, prevalences of the various parasite taxa did not present any seasonality, except for *Trichostrongylus* sp., for which prevalence was significantly higher in summer. *Trichuris* sp. and *Entamoeba coli* prevalences varied significantly between the two consecutive winter seasons. Output of *Trichuris* sp. eggs was also significantly higher in summer than winter, while no seasonality was apparent in *Oesophagostomum* sp. egg emission. In summary, there did not seem to be any seasonal pattern in parasite diversity and prevalence, and when there was a difference between seasons, summer always showed higher values than winter. Additionally, when comparing the two winter seasons, higher rainfall and hence humidity seemed to have a negative effect on parasite diversity and prevalence.

Tokai troop showed the same trend as Plateau Road. The mean helminth and protozoan diversity was significantly higher in faecal samples collected in summer. Four nematode taxa were found only in summer samples: *Trichostrongylus* sp., *Physaloptera* sp., hookworm type, and an unidentified spirurid. Whenever there was a significant variation between seasonal prevalences, the summer prevalence was higher.

The seasonal patterns in the Da Gama Park troop were mostly as predicted by theory, with helminth diversity being higher in winter. One more helminth taxa, hookworm type, was found in winter, without showing significant variation in prevalence. For the taxa that showed significant seasonal variation in prevalence, winter prevalences were higher than summer ones in most cases. Egg production, however, showed a different pattern with both *Trichuris* sp. and *Oesophagostomum* sp. having significantly higher egg output in summer than in winter.

It is difficult to establish the reasons for the opposite seasonal patterns found in different troops of the same population. Gordon (1948) and Smith (1990) found that different species of nematodes are more or less susceptible to different microclimatic conditions. However, at any particular temperature, survival has been found to be greatest when conditions are most humid (Rogers & Sommerville 1963). Hausfater and Meade (1982) found that baboons avoided contaminated sleeping sites more often in the rainy season than in the dry season and other studies of arboreal primates showed a positive relationship between moist environments and intestinal macroparasite infections (Stuart *et al*. 1993, 1998; Stuart & Strier 1995; Stoner 1996). Clearly, a field experiment is needed to prove whether local environmental conditions can explain the differences in seasonal patterns of parasite diversity and prevalence found in different troops in the Cape Peninsula.

The troop with the largest sample size across the two seasons was Plateau Road, and there were no seasonal patterns in either helminth diversity or prevalence (except for *Trichostrongylus* sp. prevalence, which was significantly higher in summer). The fact that *Trichuris* sp. egg output was higher in summer could be explained by the 2-3 month period required for this worm to develop in the host and become reproductive (Appendix D). Even if infectious stages were present in the environment at higher rates in winter, this would only be expected to manifest as a higher level of adult infection in the summer months when the worm had matured and was capable of producing eggs that would appear in the faeces.

Results from different studies in South Africa suggest that there are no clear and consistent seasonal patterns for standard parasite indices. No evidence for seasonal fluctuations in egg output was found by Appleton and Henzi (1993) in baboons ranging in Mkuzi, a location with a subtropical climate. In the Drakensberg, which has a montane climate, winter egg output in baboons was significantly higher than summer output for *Oesophagostomum* sp. *bifurcum* and

Trichuris sp. *trichiura* (Appleton & Henzi 1993). Further investigations on seasonal output of infective stages could provide more information, as well as an analysis of soil content to detect seasonal differences in nematode soil load and therefore possible seasonal effects on their survival rate.

Given the variation between seasons in the three parasite indices investigated in this study it was decided to only use samples from one season (winter) for further comparisons of parasite infections between troops.

8.2 Host-individual factors

8.2.1 Intra-individual variation

High variability was found not only in the number of parasite stages shed in faecal samples, but also in the presence of these stages in repeat samples from the same host, as proposed by Anderson and Schad (1985). It was not possible in this study to elucidate the cause of this variability. It is possible that this variation could have been due to sampling a part of the scat that contained more or less parasite stages. Collectors tried to avoid this bias by thoroughly mixing the faeces in a plastic bag prior to sampling. Another factor, not avoidable through collection methods, would be the potential variability in egg production by the parasites. Some species might release eggs or larvae intermittently while others may release eggs continuously (Anderson & Schad 1985). Such differences may translate into high variation in the number of parasite stages within a particular faecal sample and across different scats. Other explanations for intra-individual variation include temporal variation in detection of parasite stages during examination of slides. For example, Chapman (pers. comm.) found that he typically needs to examine at least five slides in order to not find any more protozoan species. This potential error was dealt in the present study by examining two replicates for each faecal sample collected. It was also established (section 8.1.2) that at least three sequential samples had to be analyzed per individual to obtain a reliable estimate of species richness. Irrespective of the actual cause, the results demonstrate once again the importance of collecting repeat samples from each host to obtain reliable estimates for individual infection rates.

8.2.2 Age and sex variations

Parasite infection was not affected by the sex of the hosts sampled and thus the prediction of higher parasite diversity and prevalence in males was not supported. Analyses on different primate species have not found any significant impact of sex on parasite prevalences (Eilenberger 1997; Mutani *et al.* 2003; Gillespie *et al.* 2004; Gillespie *et al.* 2005b). In baboons, some sex variability has been reported but it was the females that tended to show higher parasite prevalences compared to males (Hausfater & Watson 1976; Meade 1984; Müller-Graf *et al.* 1996), with only one exception (Pettifer 1984). Thus, despite differences in the phenotype of the two sexes and therefore the different probabilities of encounter with infectious stages of parasites, no sex-linked differences were observed in the chacma baboons ranging in the Cape Peninsula.

By contrast, age did appear to influence the parasite helminth infection rate within the Peninsula baboons and, similar to the findings of Dobson *et al.* (1992), older baboons had higher infection rates than juveniles. Meade (1984) found a similar age related pattern in yellow baboons from Amboseli. It is possible that an increase in helminth infection rates with the age of the host is caused by an effect of accumulation due to the fact that the nematodes identified in the Peninsula baboons can survive for one to several years in the guts of their host (Appendix D). Helminth infections acquired during the juvenile years could therefore accumulate as the individual develops to adulthood resulting in a greater parasite diversity and prevalence in adult baboons. However, two of the nematodes with the highest prevalence in adult host in this study, namely *Trichuris* sp. and *Oesophagostomum* sp., presented strong seasonality of infection at many sites (Huffman *et al.* 1997; Huffman *et al.* 2009), bringing evidence not favourable to an accumulation hypothesis. Other alternative hypotheses could include possible age differences in substrate use or in ingestion of infected soil and vegetation.

8.2.3 Reproductive status

Variations in the reproductive status of female chacma baboons did not appear to have any effect on parasite diversity, prevalence, or infective stages output. No increase in prevalence or intensity of parasite infection was detected during gestation and/or lactation compared to cycling females. The only exception to this was *Entamoeba hartmanni*, a protozoan commensal of baboons, which showed a significantly higher prevalence (49%) in lactating compared to cycling females (38%). However, prevalence of the same protozoa was the lowest for pregnant individuals (12%), suggesting that the costs associated with reproduction are not the sole explanation for the difference between lactating and cycling females. Other studies on the effects of reproductive status in baboons on parasite infection were not consistent. While some studies showed that ova emission in baboons was higher among pregnant females (Meade 1984), other studies found the opposite to be true, with higher ova emission in cycling baboon females compared to pregnant individuals (Hausfater & Watson 1976). Müller-Graf *et al*. (1996, 1997) found that *Trichuris* intensity of infection was the lowest in pregnant baboon females.

The lack of a correlation between reproductive status and parasite infection in the present study population could be associated with a number of factors including social status, food availability, and the life history traits of the parasites. Parasite infections have been shown to correlate with variations in the social status of females, which may therefore mask the effects of reproductive state in the different females. Energy demands usually increase during gestation and lactation and this demand can have an adverse effect on the functioning of the immune response resulting in higher parasite loads (Sheldon & Verhulst 1996; Klein & Nelson 1999; Bercovitch & Ziegler 2002). However, the nutritional bottleneck associated with reproduction may have been masked in this study, as the baboons included in the analysis were all semi-provisioned by virtue of having access to high quality human derived food stuffs.

8.2.4 Social status

There was a general lack of correlation between the social status of female baboons and measures of parasite infection. This is in accordance with what has been found in other baboon studies by Hausfater and Watson (1976), Meade (1984), and Müller-Graf *et al.* (1996). Prevalences of the nematodes *Trichuris* sp. and *Oesophagostomum* sp., and of the protozoa *Balantidium coli* and *Entamoeba coli* were all similarly high (i.e., 100%) irrespective of social status.

It is interesting to note that while there were significant differences in infection indices, they were not consistent with respect to rank. Thus, the prevalence of the nematode *Trichostrongylus* sp. was significantly higher in female baboons of higher rank (83%), compared to low ranking individuals (17%), and absent in medium ranking females. By contrast, the prevalence of another nematode, *Ascaris* sp., was significantly higher in low ranking individuals (50%) than high-ranking ones, in which it was completely absent. The life cycles of these two nematodes do not explain the differences, since in both cases the infective stages have to be ingested for infection to occur. However, while *Ascaris* eggs lie passively in the soil, the infective larvae of *Trichostrongylus* actively crawl up vegetation to ensure a higher chance of ingestion by hosts (Appleton 1989). Thus, it is possible that this difference in parasite behaviour could impact differently on individuals of different rank, if rank influenced where and how individuals fed within the environment that is infected with the different parasites.

8.3 Cape Peninsula inter-troop comparisons

8.3.1 Protozoa

All the protozoan taxa identified within the Peninsula population were present within all of the troops sampled, with the exception of *Endolimax nana*. It is possible that this pattern is a consequence of the smaller size of protozoan infective stages which are more easily dispersed (e.g., by wind) across the Peninsula, or by virtue of protozoa being more adaptable to a wider range of environmental conditions. In a study on olive baboons, Freeland (1979) found that all groups of a population of this primate exhibited identical protozoan faunas, possibly as a consequence of a higher rate of exchange of individuals between groups.

Even if all protozoan species were present in all the study troops, mean protozoan diversity in faecal samples presented heterogeneity between troops. Protozoan diversity was significantly lower in Tokai than all other troops. In addition, protozoan diversity for the Tokai troop differed the most from the three troops that were the furthest from Tokai and whose home ranges comprised predominantly indigenous vegetation. Tokai was the most similar to the geographically closest troop of Da Gama Park, which - similarly to Tokai - had a high percentage of exotic vegetation within its home range. The highest median protozoan diversity was found in Kanonkop, the troop with the least human contact and the most pristine indigenous vegetation. Kanonkop protozoan diversity differed significantly from Da Gama Park and Plateau Road troops, which are similar to Tokai in that they have a high percentage of exotic vegetation within their home ranges. Together these results suggest that the broad scale habitat attribute of exotic vegetation type may influence protozoan PSR. The results were confirmed when PSR and exotic vegetation were compared (Table 6.3), with a significant negative correlation between protozoan PSR and the portion of home range overlapping with exotic vegetation.

The prevalences of three protozoa varied significantly across the Peninsula population: *Entamoeba chattoni*, *Iodamoeba bütschlii*, and *Entamoeba hartmanni*. In all cases, the prevalence was significantly lower in Tokai than in the other troops. Despite the high prevalence of *Balantidium coli* in the troops studied, potential symptoms of high infection (i.e., diarrhoea or bloody-mucoid scats) were not observed.

8.3.2 Helminths

Across all troops, helminth PSR varied from zero to a maximum of six taxa. The Tokai troop hosted a significantly lower number of helminth species compared to the other troops, with the exception of the Cape Point troop. It is possible that the markedly different habitat type associated with the Tokai region may account for some of the differences in helminth PSR and prevalence in this region when compared to other regions within the Peninsula. The Tokai troop lives within an anthropogenically modified environment characterised by exotic pine and eucalyptus plantations and vineyards. The climatic conditions are also markedly different, with significantly higher rainfall than all of the other regions. Together these habitat characteristics translate into higher humidity, deeper leaf litter, and reduced light penetration associated with the dense foliage of the plantation canopy, all of which may influence the life cycle and hence infection rate of the different helminth taxa. However, according to previous studies on nematodes' life cycle (Rogers & Sommerville 1963) and on parasite infections in baboons (Hausfater & Meade 1982), environmental conditions with enhanced humidity should favour, and not negatively affect, the survival and development of infectious stages. Other significant variations between helminth diversity and troop were apparent but there were no consistent or clear patterns. There was furthermore no consistent pattern with respect to helminth diversity and different troops within the Peninsula with for example significant variation between the Cape Point and Kanonkop troops despite both occurring within the Cape of Good Hope (CoGH) section of the Table Mountain National Park (TMNP). Kanonkop was the only troop in which the unidentified spirurid was found. The prevalences of three helminth taxa varied significantly across study troops: *Trichuris* sp., *Oesophagostomum* sp., and *Physaloptera* sp. (Figure 6.3), with both *Trichuris* sp. and *Oesophagostomum* sp. being found in every troop sampled in this study. The ubiquity of these nematodes may be a consequence of the higher rate of infective stages they produce (310 and 104 eggs/g on average for *Trichuris* sp. and *Oesophagostomum* sp., respectively) relative to the other helminth species found in the Peninsula baboons (6, 35 and 10 eggs/g on average for *Trichostrongylus* sp., *Physaloptera* sp., and *Ascaris* sp., respectively). The prevalences of *Trichuris* sp. and *Oesophagostomum* sp. are also positively correlated (see below) suggesting that a positive association could exist between them, or at least that they do not compete against each other when occupying the same host. Moreover, the majority of faecal samples analyzed in this study (61%) were infected with more than one species of helminth (maximum two or three taxa). Various studies have found evidence of synergistic interaction between helminth species in a host, although the role of interspecific parasite interactions is still unclear (Lello *et al.* 2004; Behnke *et al.* 2005; Fleming *et al.* 2006). This is an important factor to consider since the existence of competition between different helminth taxa in the same host could also have an impact on the severity of infections, thus potentially acting as a confounding factor. It was not possible to establish what conditions may favour the transmission and infection rates of *Trichuris* sp. and *Oesophagostomum* sp. in the Cape Peninsula baboons. The longer life span of these two nematodes (one to three or more years; Adams *et al.* 2005) compared to other nematodes like *Ascaris* (about one year) could explain in part their higher prevalences (i.e., through a cumulative effect).

Ascaris sp., a nematode potentially linked to proximity to humans, was found in five of the six troops analyzed, including Kanonkop, the troop with the lowest rate of human contact. The prevalences of *Ascaris* sp., *Trichostrongylus* sp., hookworm type, and the unidentified spirurid did not differ significantly across the study troops. *Trichostrongylus* sp. prevalences were low and similar among troops (except for Tokai, where it was not found). Hookworm type and unidentified spirurid were found only in two and one troop respectively and with very low prevalences.

In summary, the distribution of helminth taxa across troops was over-dispersed, as is characteristic of the majority of macroparasite-host associations (Crofton 1971). Levels of prevalence differed between contiguous troops, suggesting that differences in micro-habitat or other characteristics specifically related to a troop but not measured in this study may be important. In addition, while the intestinal helminth infection varied significantly among the six study troops, there was more variation in the mean prevalence levels among the different parasite species. Two parasite species (*Trichuris* sp. and *Oesophagostomum* sp.) had consistently high prevalence across all troops while three parasites (*Trichostrongylus* sp., *Physaloptera* sp., and *Ascaris* sp.) were found at consistently lower levels in all troops. Only two parasite species (hookworm type and unidentified spirurid) were rare or absent from most troops. Thus, prevalence levels of each helminth parasite appear to be similar irrespective of the troop they occur in (see Figure 6.3) suggesting that prevalence levels could be linked to the particular attributes of the parasite and not the troop. Another possible explanation is that the relative environmental and seasonal differences across the study sites were not large enough to bring about greater variation in prevalence than what was found.

8.4 Influence of troop attributes on parasite infection

8.4.1 Correlations between troop attributes

Most of the twelve troop attributes (independent variables) included in the correlation matrix between prevalence and ecological attributes showed at least one significant correlation with other troop attributes (dependent variables) (see Appendix G). Most of these significant correlations were expected based on our understanding of the ecology of baboons. Thus, for example, home-range size was negatively correlated with the intensity of use of the home range and the number of sleeping sites was positively correlated with the troop size. Similar findings have been reported by Hamilton (1982), who showed that a large troop is forced to use a bigger home range to obtain enough food, and will therefore use a larger number of sleeping sites to minimise time spent travelling to new foraging areas. One correlation that was expected was the increase in the proportion of human food in the diet with an increase in the percentage of overlap of a troop's home range with urban land.

8.4.2 Correlations between parasite infection and troop attributes

Group size and host density

PSR and prevalence were expected to correlate positively with group size and host density. Larger group size was predicted to lead to greater faecal quantities and soil contamination with parasite infectious stages, and therefore higher risk of gastrointestinal parasite infections. The results did not support this hypothesis as no effect of group size on helminth and protozoan diversity or the prevalences of the five nematode species analyzed was found. Few studies on primates have shown a significant association between group size and parasite infections (e.g., Freeland 1979; McGrew *et al.* 1989). The present results are in accordance to what has been found in comparative studies, which revealed only few links between social group size and PSR in primates (Nunn *et al*. 2003; Vitone *et al*. 2004). In a study on red howling monkeys (*Alouatta seniculus*), Gilbert (1994) did not find any correlation between group size and parasite prevalence, while Chapman *et al.* (2005b) found opposite patterns between *Trichuris* sp. prevalence in colobine monkeys and group size between two consecutive study periods. Interestingly, Snaith *et al.* (2008) found that group spread was negatively related to parasite infection prevalence and suggested that group spread increased because of food competition. Increased group spread may decrease parasite transmission rates and thus larger groups may have lower infection rates simply as a by-product of increased competition. In this study, the troop with lowest density that typically spread over a very large area when foraging was Kanonkop, which had the highest PSR and similar levels of prevalence to troops with a higher density that foraged in closer proximity.

Host density clearly did not have an impact on nematode infections in the Cape Peninsula baboons but correlated negatively with protozoan PSR and with *Trichostrongylus* sp. prevalence. Other studies have reported similarly unexpected results of higher helminth infection levels at lower host density, but no clear negative correlation has been found in protozoan diversity. Chapman *et al.* (2005b) did not find evidence of a correlation between colobine monkeys' density and helminth PSR, except for *Trichuris* sp. prevalence. Stuart *et al.* (1993) reported higher PSR and prevalences in the population of muriquis (*Brachyteles arachnoides*) with the lowest density, while Müller (2007) could not find any correlation and attributed this to the subordinate role played by demographic factors in influencing indirect and soil-transmitted parasite infections. In a study on black howler monkeys (*Alouatta pigra*), Vitazkova and Wade (2007) detected higher nematode prevalence of a nematode in populations with lower host densities. Ecosystem disturbance was pinpointed as a possible explanation of this pattern, with human activities disrupting the ecological web involved in parasite transmission. Gillespie and Chapman (2006) suggested that anthropogenic activities could have an influence on host density and, therefore, parasite infection through the reduction of habitat area for primate populations. Protozoan diversity among the Cape Peninsula population was the highest in the Kanonkop troop, which was the troop with the least human disturbance. On the contrary, protozoan diversity was lower in one of the troops more affected by anthropogenic changes, namely the Tokai troop. Human disturbance cannot therefore be used as an explanation for the negative correlation between protozoan diversity and host density in this study. Other reasons could include the dispersion patterns of protozoan parasites in the Cape Peninsula or the success rate of parasite establishment in the host after infection, factors that were not investigated in this study. The general trend in social mammals studied to date is a positive correlation between host density and parasite prevalence and diversity (Gilbert 1994; Ghandour *et al*. 1995; Arneberg *et al*. 1998; Morand & Poulin 1998; Arneberg 2001; Nunn *et al*. 2003). Group size and host density are known to play a more important role in directly transmitted parasites (Côté & Poulin 1995; Altizer *et al*. 2003) and the Cape Peninsula parasites are all transmitted through infective stages that are dispersed in the soil. In summary, the patterns of infection of the parasites found in this study did not seem to be influenced by host group size and density.

Home-range size and intensity of use

PSR was predicted to be higher in troops with larger home ranges, while prevalence was predicted to be lower. Troops using parts of their home range more intensively were predicted to show increased parasite prevalence due to higher opportunities for reinfection. The results of this study did not provide support for either of these predictions. There was no correlation between home-range size and intensity of use of the home range in either parasite diversity or the prevalence of soil-transmitted nematodes. Results from other studies have provided contradictory results. A study on gorillas by Eilenberger (1997) showed a positive association between intensity of reuse of the home range and parasite infection. In a comparative study on primates, Nunn *et al.* (2003) found a negative correlation between home-range size and helminth parasite diversity. A similar result was found by Gilbert (1994) in red howling monkeys. Similar to this study, Müller (2007) found no significant relationship between PSR and home-range size in baboons, while Stuart *et al.* (1993) found a positive correlation between home-range size and PSR and prevalence in a field study on muriquis and brown howling monkeys (*Alouatta fusca*). Vitone *et al.* (2004) found a positive association between the diversity of indirectly-transmitted helminths and home-range size in 69 primate species. Together these studies suggest that there is no clear and consistent pattern between parasite indices and home-range size in primates. Surprisingly, despite the marked influence of humans on the patterns of home-range use in monitored troops (e.g., Da Gama Park and Cape Point), there was no measurable difference in parasite infections compared to non-monitored troops.

Overlap between troops

Parasite diversity and helminth prevalence were expected to be greater in baboon troops with a larger number of neighbouring troops and greater range overlap. Protozoan PSR and the prevalence of the helminth *Trichostrongylus* sp. correlated positively with the total number of overlapping troops. With the exception of *Ascaris* sp., helminth prevalence showed a positive relationship with both the number of overlapping troops and the proportion of home range shared between troops. A similar result was obtained for a study on gorillas (Eilenberger 1997), with the group with the most overlapping home range and shortest daily movement being the most infested with parasites. On the contrary, a comparative study of PSR in relation to primate home-range overlap produced no significant results (Nunn & Dokey 2006). Contact between baboon troops in the Cape Peninsula occurs indirectly when group ranges overlap, providing the means for parasites to spread through contact with soil contaminated by other troops. Dispersal of baboon males between troops could represent another route for parasites to be passed from one troop to the next. For example, the entrance of a non-group member into a group of blue monkeys resulted in an increase in the PSR of the group's protozoan fauna (Freeland 1979). Freeland (1979) also suggested that different groups of baboons harbour more protozoa than do rainforest monkeys, because transfer of individuals between groups occurs more commonly in baboons. In conclusion, interaction between troops in the Cape Peninsula baboons, either directly through male dispersal or indirectly through home-range overlap, positively affected indices of parasite infection.

Home-range overlap with urban and transformed land

Parasite PSR and helminth prevalences were predicted to associate positively with the percentage of overlap of a troop's home range with urban and transformed land. This prediction was not supported by the results of this study, as there were no significant correlations with parasite infection and the percentage of overlap with urban or transformed land in the Cape Peninsula. In fact, protozoan PSR and *Trichostrongylus* sp. prevalence even showed significant negative relations with percentage of overlap with transformed land. Several studies on primates have shown a positive correlation between the degree of human contact and the degree of primate parasite infection (Ghandour *et al.* 1995; Müller-Graf *et al.* 1997; Munene *et al.* 1998; Wallis & Lee 1999). It is not clear yet if this is due to cross-transmission of parasites from humans to baboons or to other as yet unknown troop characteristics that are influenced by human activity. The percentage of transformed land within a troop's home range is not an accurate proxy for the degree of human contact. Thus, for example, both the Buffels Bay and Cape Point troops living within the CoGH section of the TMNP had a low percentage of transformed land within their home range but high levels of human contact with tourists. Furthermore, transformed land often equates to improved food availability as both urban and agricultural land-use typically results in improved above ground biomass of vegetation and hence greater primary productivity. Improved nutritional quality may result in reduced host susceptibility to parasites and thus, despite higher exposure to potential cross-parasite transmission routes, may offset infection rates. It is nevertheless important to understand how patterns of parasitism in wild hosts are influenced by interspecific contact rates (Nunn *et al.* 2003) and to know if parasite cross-transmission between nonhuman primates and humans (and their domesticated animals) is possible. This will be addressed below.

Presence of monitors and anthropogenic food sources

The daily herding of selected troops by monitors along well-established routes and to specific sleeping sites was predicted to result in higher exposure to the infective stages of parasites and hence correlate positively with helminth prevalence. Prevalence was also predicted to be lower in troops with a higher proportion of human food in their diet, due to improved nutritional status. Results did not show any effect of either the presence of monitors or the index of human food in the diet of a troop on any of the parasite variables investigated. Monitors effectively strive to reduce the percentage of overlap between the home range of a troop and both transformed land and human derived food. However, the very act of monitoring brings baboons into regular and close contact with humans and may thus increase the exposure of both baboons and humans to cross-transmission of parasites thus confounding the predicted effect of monitors on baboon infection levels.

Food shortage in baboons has been shown to correlate with high prevalence of helminths (Appleton & Henzi 1993) and it has been suggested that primates that raid agricultural crops may improve their condition, increase immunity to infection, and decrease pathogen impacts on host survival and reproduction (Eley *et al.* 1989). Hahn *et al.* (2003) found that some spirurid nematodes had increased prevalence in olive baboon troops that supplemented their nutrition by feeding on refuse, while others had decreased prevalence. Human food is available to all troops in the Peninsula with the exception of Kanonkop. The high helminth and protozoan PSR in Kanonkop, which has neither access to human derived foods nor exposure to monitors, suggests that neither variable is likely to have a strong positive influence on parasite infection in the Peninsula baboons.

Number of sleeping sites

PSR and helminth prevalence was predicted to correlate negatively with the number of sleeping sites used by a given troop. The results however did not support the prediction. There was no effect of the number of sleeping sites used by each troop on either PSR or helminth prevalences in troop members. The only exception to the latter was the prevalence of *Ascaris* sp., which, contrary to my prediction, correlated positively with the number of sleeping sites used. Results are conflicting in the literature as well. A few studies (Hausfater & Meade 1982; Hausfater & Sutherland 1984; Meade 1984) demonstrated that parasite larvae were present at higher density in the soil beneath baboon sleeping sites. By contrast, two other studies (Anderson & McGrew 1984; Hahn *et al.* 2003) revealed that troops of baboons that used a single sleeping site or few sleeping sites at a higher rate had levels of parasitism similar to other groups in the same populations. In conclusion, the selection of sleeping sites (number and frequency of use) does not appear to correlate with levels of parasite infection in the troops investigated in this study. In has been suggested that sleeping sites play different roles in different species, or even among populations of the same species, in particular in the avoidance of predation and proximity to food resources (Nunn & Altizer 2006). For example, the fact that the number of sleeping sites correlated negatively with the percentage of overlap with transformed land could be a consequence of a preference for a sleeping site that is closest to areas of higher quality of food resources (e.g., human food), and thus the troop members may have better nutritional status and lower levels of parasitism compared to troops that use many sleeping sites but do not have access to high quality food (e.g., Kanonkop).

Rainfall

PSR and helminth prevalence were predicted to correlate positively with rainfall as the infective stages in the soil thrive under conditions of high humidity. Rainfall however correlated negatively with protozoan diversity and the prevalence of *Trichostrongylus* sp.. Other studies have found no differences due to seasonality - and therefore rainfall - and the presence of macroparasites (intestinal parasites in chimpanzees, McGrew *et al.* 1989; and schistosome in baboons, Müller-Graf *et al.* 1997). Rainfall could also potentially clear away pathogens. Meade (1984) found that spirurid nematode prevalence increased in the dry season. More interestingly, Pettifer (1984) found that in chacma baboons the hookworm *Trichostrongylus falculatus* was more common in the dry season. The same trend was found in this study, suggesting that the infective stages of this nematode are negatively affected by high humidity and/or the low temperatures that characterise the Cape Peninsula during the winter months. Resistance of infectious stages to environmental degradation varies between parasite species. For example, the eggs of some parasites, such as the nematodes *Trichuris* and *Ascaris*, are resistant to desiccation due to their thick shells (Meade 1984) and thus likely to be present in both wet and dry conditions. Another abiotic factor, wind, could play an important role in infection probability. The Cape Peninsula is renowned for its high winds, particularly during the summer months, and it has been established that the eggs of certain parasites (e.g., *Ascaris*) may be wind-borne and thus capable of infecting individuals at great distance from the original host. Clearly, there are many abiotic factors in addition to rainfall that influence the seasonal fluctuations in parasite prevalence and PSR that need to be considered in future studies.

In summary, there were few significant correlations between helminth/protozoan PSR and helminth prevalence and the 12 ecological variables investigated in this study. Furthermore, the significant correlations rarely supported the predictions outlined in the introduction and based on the detailed literature review in Chapter 2. It is possible that I failed to measure other key ecological variables that might better explain the variation in diversity and prevalence of the different parasites in the six Peninsula troops. In addition, other statistical methods (e.g., principal component analysis) could be used along multiple comparisons to reveal patterns in the data missed with bivariate tests. However, all of the variables considered in this study have been investigated in other studies and there are no key variables that have been shown to be important in other primate/parasite studies that have been omitted from this study.

8.5 Host specificity: *Trichuris* sp.

In this study, we have demonstrated that baboons in at least one of the troops living on the Cape Peninsula harbour a well-defined genetically different species of *Trichuris* from humans and that this species can be reliably identified by its ITS1 and ITS2 sequences. This new species has been called *T. papionis*, reflecting its origin in baboon hosts. This was the first time that a *Trichuris* specific to a nonhuman primate species has been identified. Perhaps even more surprising was that the *Trichuris* worms isolated from the two other troops of baboons in the Cape Peninsula (Cape Point and Groot Olifantsbos troops) were more closely related to the *Trichuris* isolated from a human host (*T. trichiura*) in central Africa than to the *Trichuris* isolated from the neighbouring baboons in the Da Gama Park troop (*T. papionis*). It is likely that *T. trichiura* worms from Cape Point and Groot Olifantsbos baboons are a result of a reverse zoonotic infection of baboons with human whipworms. Although a small sample of baboons was used in this study, we have identified two genetically distinct *Trichuris*, one that is the original baboon parasite (*T. papionis*), and another (named *T._trichiura*_host_*Papio_ursinus*) that strongly resembles the human *Trichuris*.

This study challenges the suggestion of a high degree of host specificity in primate helminths as proposed by Pedersen *et al.* (2005) and perhaps more importantly, suggests a link between the infection of *T. trichiura* in humans and baboons. In this study, it was not possible to elaborate the proportion of *T. papionis* and *T. trichiura* in the baboon troops. It would be of high interest to determine this, in order to understand if the high prevalence (66% across all troops) of *Trichuris* sp. in the Cape Peninsula could be viewed as a consequence of cross-transmission of *T. trichiura* from the human population. Additional work could include, for example, the screening of 10 baboons from each population's troop and work out whether they are infected with human or baboon *Trichuris*. From a human health point of view, baboons could act as a reservoir for *T. trichiura* in areas with a high degree of contact between baboons and humans, although this still remains to be proven by future studies. Likely areas for cross-transmission of parasites suggested by various authors are: communal water holes (Hausfater & Sutherland 1984), human refuse and food wastes, including animal parts (Rolland *et al.* 1985; Hahn *et al.* 2003), and soil (Muriuki *et al.* 1998). In the Cape Peninsula, baboons regularly access residential areas and have both direct and indirect (through faeces) contact with gardens and houses. From a management perspective, the finding that baboons and humans may both serve as hosts to *T. trichiura*, and hence could increase infection in one another, provides conservation authorities and town planners alike with a strong argument to restrict the spatial overlap between the human and baboon populations of the Cape Peninsula.

Further studies should investigate the morphological differences between eggs and adult worms of *T. papionis* and *T. trichiura* using optical microscopy and scanning electron microscopy (SEM). This type of biometric studies was used successfully by Cutillas *et al.* (2009) to investigate the similarity between *T. trichiura* and *T. suis*.

The molecular analysis of *T. trichiura* isolated from human patients in the Cape Peninsula represents the next single most important step in this investigation of patterns of parasite infection as it could provide definitive evidence of cross-transmission of this nematode between humans and baboons. The *T. trichiura* sequence that we found in *Trichuris* isolated from baboons of the Cape Point and Groot Olifantsbos troops (*T._trichiura*_host_*Papio_ursinus*_CP_GOB) was slightly different from the *T. trichiura* isolated from humans from Cameroon. *T. trichiura* isolated from nonhuman primates by Cutillas *et al.* (2009) was even less similar to the human *T. trichiura* sequence than the whipworm isolated from the CP and GOB troops of baboons. A molecular analysis of *T. trichiura* isolated from human patients in the Cape Peninsula would help in clarifying the differences attributed to natural variation within population variations of the same species. Additional sequencing of isolates taken from *T. trichiura* from human patients would help in the establishment of the range of expected population variation of *T. trichiura*.

Finally, the same type of molecular analysis on other helminth and protozoan parasites found in baboons, other nonhuman primates, and humans could greatly improve our understanding of the mechanisms of cross-transmission between humans and nonhuman primates. The presence of *Ascaris sp.* in the Cape Peninsula baboon population may represent another example of cross-transmission with humans, since it has only rarely been found in baboons (Nasher 1988; Eley *et al.* 1989; Ocaido *et al.* 2003; Hope *et al.* 2004) and in all cases its presence was linked with some degree of human contact.

8.6 Conclusions, management implications, and future research

This study showed that helminth and protozoan species richness in the Cape Peninsula population is similar to what has been reported in other South African baboon populations. Moreover, the overall similarity of the gastrointestinal parasites among the various species of baboons across Africa suggests the presence and predominance of generalist parasites. While the diversity of intestinal helminths and protozoa were similar in different populations in South Africa, prevalences calculated for helminths in the present study were typically similar to or lower than prevalences recorded in other South African study sites. Climatic conditions are regarded as an important factor affecting the survival of parasite infective stages and thus the rate of infection of baboons. It is therefore possible that much of the variation in prevalences for one taxon among various study sites is a function of the variety of climatic conditions found in the different localities.

The distribution of helminth and protozoan taxa varied significantly among and within the six study troops in the Cape Peninsula baboon population. Heterogeneity of helminth species richness across social groups is characteristic of macroparasite-host associations and is often the result of the aggregated distribution of parasites from the same species among hosts due to differences in individual exposure, innate susceptibility to infection, and/or acquired immunity (Crofton 1971). Despite the small number of troops compared, a trend appeared in the distribution of parasite infections. Two troops, Kanonkop and Da Gama Park, showed the highest helminth and protozoan species richness and the highest prevalence of the nematodes *Trichuris* sp. and *Oesophagostomum* sp.. By contrast, a third troop, Tokai, scored the lowest level of parasite species richness and the lowest prevalences of the same two nematodes. These results are somewhat surprising because while both the Da Gama Park and Tokai troops are subject to strong human influence, their parasite infections are at the opposite ends of the Cape Peninsula's spectrum of infections. Moreover, it was surprising to find the highest levels of parasite infection in Kanonkop, the troop ranging in the most pristine habitat in the Cape Peninsula and with the lowest level of human contact.

Various factors specific to the troop, the environment, and the level of anthropogenic disturbance were investigated in an attempt to explain variation in parasite infection levels across the six study troops. However, despite including all of the variables that have to date been shown to influence infection rates in both other studies on chacma baboons and other primate species, only few variables correlated significantly with infection rates across all study troops. Thus, protozoan species richness was negatively correlated with host density, degree of home range overlapping with transformed land, and rainfall and positively correlated with the number of troops that overlapped with a given troop. *Trichostrongylus* sp. prevalence showed the same trend, being also negatively correlated with host density and degree of home range overlapping with transformed land, and positively correlated with the number of troops that overlapped with a given troop. None of the variables associated with anthropogenic disturbance were found to correlate positively with parasite infection rates. In summary, there were no clear and consistent relationships between troop attributes and the mean prevalence or total species richness across all troops. Furthermore, there was no single troop attribute that influenced the prevalence of the respective helminths in a clear and consistent manner, providing support for Price (1980), who stated that no single factor can be expected to dominate the distribution of all parasites.

Despite the lack of significant correlations in this study, there were nevertheless some important findings that warrant future further detailed investigation. Thus, the high levels of parasite infection in the most undisturbed troop, Kanonkop, might be linked to the low nutritional quality of the food within their home range. The Kanonkop troop's home range is comprised almost exclusively of indigenous fynbos vegetation, which is known to be both low in productivity and nutrients. The significantly longer mean daily distance travelled and larger home-range size of the Kanonkop troop (Hoffman unpubl. data), in addition to the slow annual growth rate of the troop (Beamish unpubl. data) relative of to all other troops on the Peninsula, supports the suggestion that the quality of food within the home range of this troop is lower than in other troops and thus troop members have much higher foraging costs. Furthermore, Kanonkop is the only troop in this study that has no access to human derived food and/or exotic vegetation, both of which provide a diet that is higher in caloric value and nutrients. Together these findings suggest that the Kanonkop troop members have a poor nutritional status relative to baboons in other troops on the Peninsula. Poor nutritional status is known to have an adverse effect on the functioning of the immune response, which in turn has been shown to result in higher parasite loads (Sheldon & Verhulst 1996; Klein & Nelson 1999; Bercovitch & Ziegler 2002). Importantly, Eley *et al.* (1989) found that groups of baboons raiding agricultural crops showed lower intensities of parasitism compared to the groups foraging on natural resources, and suggested that improved nutrition may facilitate a more effective immune response.

Chronic stress has been shown to have an adverse effect on host immune function and may thus be an important determinant of overall fitness (Chapman *et al.* 2007; Snaith *et al.* 2008). Peninsula troops that have been forced into high levels of human interaction as a result of competition for limited suitable space were expected to suffer higher levels of stress, reduced immune functioning, and thus greater parasite burdens. However, proximity to humans may have the advantage of access to higher quality food, which may offset the costs associated with the stress of raiding and thus lead to ambiguous correlations between host parasite infections and anthropogenic influences. With clearing of exotic vegetation and improved management to keep baboons out of urban areas, it is likely that these troops will have greatly reduced access to these high quality food sources but will still have conflict with the humans who are responsible for keeping them out of the urban area, namely the monitors. It will thus be important to perform a follow up study and assess whether reduced food quality with similar stress levels results in elevated levels of parasitism, comparable to or higher than the Kanonkop troop. The results of one such study would be pivotal to disentangling the complex interactions between anthropogenic effects, nutritional status, and parasite infection levels in chacma baboons.

It is possible that the lack of any single factor explaining a significant amount of the observed variation in parasite infection levels between troops of the Cape Peninsula baboon population could be a consequence of the biology of the parasites themselves. Prevalence levels of specific helminth parasites appear to be similar irrespective of the troop they occur in, suggesting that prevalence levels may be linked to the particular attributes of the parasite and only marginally influenced by the troop attributes. Thus, two parasite species (*Trichuris* sp. and *Oesophagostomum* sp.) had consistently high prevalence across all troops while three parasites (*Trichostrongylus* sp., *Physaloptera* sp., and *Ascaris* sp.) were found at consistently low prevalences in all troops. Clearly, further investigation into the parasites' attributes, in particular on the survival rate of their infectious stages in different conditions (e.g., different microclimates, soil types, specific vegetation types) across the Cape Peninsula, is needed to shed light on the observed variations between parasite species across all troops. In addition, the possible existence of competition or synergic interactions between different helminth taxa in the same host might have an impact on infection levels, and therefore confound analyses that only explore the hosts attributes or possible environmental factors. Co-infection with multiple parasite taxa could therefore be analyzed in more detail by using multivariate analyses to search for significant associations between parasite taxa in the same host.

The high prevalence of *Trichuris* sp. and *Oesophagostomum* sp. in the troop with the highest exposure to urban areas, namely Da Gama Park, suggests that infection rates may be affected by prolonged contact with urban areas. Chapman *et al.* (2006a) suggested that monkeys ranging along forest edges may have increased parasitism stemming from frequent contact with humans. It is however very important to complement such suppositions with genetic and morphological analyses of the actual parasites (Mbora *et al.* 2009). This study, similar to that of De Gruijter *et al.* (2005a) working on *Oesophagostomum bifurcum*, demonstrated for *Trichuris* sp. that parasites that infect sympatric humans and monkeys can constitute genetically distinct populations according to host species. Furthermore, evidence is provided in Chapter seven for cross transmission of the human whipworm, *Trichuris trichiura*, to baboons within the Groot Olifantsbos and Cape Point troops of the Cape Peninsula.

The lack of fundamental research on the Cape Peninsula baboon population has, to date, hampered the implementation of informed and effective management policies. The baseline data on species diversity and prevalence of gastrointestinal parasites of the baboons presented for the first time in this study provides an important first step in the disease risk assessment for conservation and management plans of this threatened population. The most important finding in this sense is the presence of the human whipworm (*T. trichiura*) in baboons of two troops within this population. The ubiquity of this parasite in the population as a whole is an important area for future research as the transmission of this nematode from humans to baboons is a concern for the conservation of baboons in the Cape Peninsula. Furthermore, the potential sources of cross-infection (e.g., communal water sources (Hausfater & Sutherland 1984), human refuse and food wastes, including animal parts (Rolland *et al.* 1985; Hahn *et al.* 2003), and soil (Muriuki *et al.* 1998)) need to be investigated in more detail to reduce further cross contamination in the population. In the interim, the evidence for cross transmission of parasites provides conservation authorities and town planners alike with a strong motivation to restrict the spatial overlap between the humans and baboons in the Cape Peninsula and indeed other regions of the Western Cape.

Urbanisation is a worldwide phenomenon and yet only a few studies to date have investigated how wildlife-pathogen interactions respond to the urban landscape (Bradley & Altizer 2006). This thesis contributes to a better understanding of how urbanisation influences parasite infections in nonhuman primates and sheds new light on the potential transmission of infectious agents among wild nonhuman primates or between nonhuman primates and humans. Future research is needed to better understand the ecology of wildlife pathogens in urban environments as this is becoming increasingly important for managing disease risks to wildlife and, in some cases, humans.

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APPENDIX A: Diversity and prevalence of gastrointestinal parasites of *Papio* spp. at different localities within Africa. Shaded areas represent parasite taxa found in the Cape Peninsula baboon population.

	Papio ursinus (chacma baboon)												
Helminths	**Cape Peninsula**	**Pringle Bay**	**Wildcliff NR**	**Giant's Castle GR (1)**	**Mkuzi GR (2)**	**Suikerbosrand NR (3)**	**Loskop Dam NR (3)**	Kruger NP (4)	**Scrutton PNR (3)**	**Northern Transvaal (5)**	**South Africa (6)**	Zimbabwe (7)	Kuiseb River Namib (8)
Nematoda													
Trichuris sp.	66	89	98	57[a]	6[a]	-	2	-	-	4	22	4	-
Oesophagostomum sp.	61	91	38	49 *	15[b]	100[b]	95[b]	79[b]	100[b]	63	-	69[b]	-
Trichostrongylus sp.	6	100	48	-	1[d]	92[d]	30[d]	100[c]	44[d]	8	11	8	-
Physaloptera sp.	8	54	78	44[e]	2[e]	10[e]	97[e]	10[e]	78[e]	4[e]	12	8	-
Ascaris sp.	9	-	-	-	-	-	-	-	-	-	-	-	-
Streptopharagus sp.	-	14	-	1[f]	30[f]	96[f]	88[f]	25[g]	100[f]	4	3	45[f]	63[f]
hookworm type	1	-	34	-	-	-	-	-	-	-	-	-	13
Spiruridae sp.	1	-	-	-	5	-	-	-	-	-	-	-	-
Ternidens deminutus	-	-	-	-	7	-	-	Present	-	4	-	57	-
Strongyloides sp.	-	-	-	-	23[h] / 6[i]	20[h]	-	41	-	38[h] / 4[i]	-	39[h]	19
Enterobius sp.	-	-	-	6	1	-	3	-	83	-	-	22	-
Cestoda													
Bertiella studeri	-	-	-	10	4	52	48	12	56	4	3	4	-
Taenia sp.	-	-	-	-	-	-	-	Present	-	-	-	-	-
Hymenolepis sp.	-	-	-	-	-	-	-	-	-	-	-	-	-
Trematoda				-									
Schistosoma sp.	-	-	-	-	2	-	-	Present	-	-	-	2	-

NR=Nature Reserve; GR=Game Reserve; NP=National Park; PNR=Private Nature Reserve; (a) *T. trichiura*, (b) *O. bifurcum*, (c) *T. colubriformis*, (d) *T. falculatus*, (e) *P. caucasica*, (f) *S. pigmentatus*, (g) *S. armatus*, (h) *S. fuelleborni*, (i) *S. stercoralis* (*) prevalence includes *Ternidens deminutus*, (**) prevalence includes all Strongylidis (*Oesophagostomum* sp., *Trichostrongylus* sp., *Ternidens* sp., etc.)

References: (1) Appleton *et al*. 1986, (2) Appleton *et al*. 1991, (3) Pettifer 1984, (4) McConnell *et al*. 1974, (5) Goldsmid & Rogers 1978, (6) Myers *et al*. 1971, (7) Goldsmid 1974, (8) Appleton & Brain 1995.

APPENDIX A continued

Protozoa	*Papio ursinus* (chacma baboon)												
	Cape Peninsula	**Pringle Bay**	**Wildcliff NR**	**Giant's Castle GR (1)**	**Mkuzi GR (2)**	**Suikerbosrand NR (3)**	**Loskop Dam NR (3)**	Kruger NP (4)	**Scrutton PNR (3)**	**Northern Transvaal (5)**	**South Africa (6)**	Zimbabwe (7)	Kuiseb River Namib (8)
Balantidium coli	100	77	66	26	80	n/a	n/a	Present	n/a	54	46	n/a	44
Entamoeba coli	91	94	92	70	75			Present		54	37		100
Entamoeba histolytica	12 (dispar)	6	2	-	-			-		-	3		25
Entamoeba chattoni	16	6	28	-	-			-		-	15		-
Entamoeba hartmanni	38	17	16	-	-			-		-	11		69
Entamoeba sp.	-	-	-	-	-			Present		4	53		-
Iodamoeba butschlii	49	40	72	2	9			Present		4	22		50
Endolimax nana	2	-	-	10	13			-		-	11		19
Chilomastix mesnili	18	29	10	13	-			-		4	-		63
Giardia sp.	-	-	-	-	-			-		-	-		25
Dientamoeba fragilis	-	-	-	-	-			-		-	-		-
Toxoplasma gondii	-	-	-	-	-			Present		-	-		-
Toxoplasma sp.	-	-	-	-	-			Present		-	-		-
Sarcocystis sp.	-	-	-	-	-			Present		-	-		-
Hepatocystis simiae	-	-	-	-	-			Present		-	-		-
Trichomonas sp.	-	-	-	-	-			-		4	-		-
Cryptosporidium sp.	-	-	-	-	-			-		-	-		-
Eimeria sp.	-	-	-	-	-			-		-	-		-

n/a = data non available; NR=Nature Reserve; GR=Game Reserve; NP=National Park; PNR=Private Nature Reserve

References: (1) Appleton *et al*. 1986, (2) Appleton *et al*. 1991, (3) Pettifer 1984, (4) McConnell *et al*. 1974, (5) Goldsmid & Rogers 1978, (6) Myers *et al*. 1971, (7) Goldsmid 1974, (8) Appleton & Brain 1995.

	***Papio anubis* (olive baboon)**												
	Kenya						Kenya & Tanzania	Tanzania			Uganda		Ethiopia
Helminths	Mpala group (1)	Kilifi (2)	Kimani (2)	Mau Narok (2)	Gilgil (3)	various sites (4)	Kenya & Tanzania (5)	Gombe (6)	Gombe (7)	Gombe (8)	Bwindi forest (9)	West Bugwe FR (10)	Rift Valley (11)
Nematoda													
Trichuris sp.	-	17	47	17	Present	74	15	42	81	66	16	-	27
Oesophagostomum sp.	40 **	100	11	83	Present	76	77	42	36	17	-	9	10
Trichostrongylus sp.	-	-	-	-	Present	44	8	-	**	-	-	61	9
Physaloptera sp.	-	-	79	-	-	-	46	44	66	23	-	-	-
Ascaris sp.	-	-	-	-	Present	-	-	-	-	-	79	21	-
Streptopharagus sp.	-	33	42	-	-	42	46	35	67	48	-	-	-
hookworm type	-	-	-	-	-	-	8	-	**	44	-	36	-
Spiruridae sp.	-	-	-	-	-	-	-	-	-	-	-	-	-
Ternidens deminutus	-	-	-	-	Present	-	-	-	-	-	42	-	-
Strongyloides sp.	76	-	-	-	Present	63	-	58	69	25	37	61	37
Enterobius sp.	12	-	-	-	-	30	-	-	-	-	-	5	-
Cestoda													
Bertiella studeri	-	17	16	28	-	-	8	-	-	-	-	-	-
Taenia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-
Hymenolepis sp.	-	-	-	-	-	-	-	-	-	-	7	-	-
Trematoda													
Schistosoma sp.	2	-	-	-	-	4	8	-	21	3	-	-	20

FR=Forest Reserve; (*) prevalence includes *Ternidens deminutus*, (**) prevalence includes all Strongylidis (*Oesophagostomum* sp., *Trichostrongylus* sp., *Ternidens* sp., etc.)

References: (1) Hahn *et al.* 2003, (2) Kuntz & Myers 1967, (3) Eley *et al.* 1989, (4) Munene *et al.* 1998, (5) Kuntz & Myers 1966, (6) McGrew *et al.* 1989, (7) Müller-Graf *et al.* 1996, (8) Murray *et al.* 2000, (9) Hope *et al.* 2004, (10) Ocaido *et al.* 2003, (11) Legesse & Erko 2004.

APPENDIX A continued

	***Papio anubis* (olive baboon)**												
	Kenya						Kenya & Tanzania	Tanzania			Uganda		Ethiopia
Protozoa	Mpala group (1)	Kilifi (2)	Kimani (2)	Mau Narok (2)	Gilgil (3)	various sites (4)	Kenya & Tanzania (5)	Gombe (6)	Gombe (7)	Gombe (8)	Bwindi forest (9)	West Bugwe FR (10)	Rift Valley (11)
Balantidium coli	n/a	Present	Present	Present	n/a	41	6/13	42	20	-	-	-	-
Entamoeba coli		Present	Present	Present		78	8/13	n/a	76	34	-	58.9	83
Entamoeba histolytica		Present	Present	Present		26	3/13	-	in *E. coli*	-	-	58.9	17 (*hist/disp*)
Entamoeba chattoni		-	-	-		-	-	-	-	-	-	-	-
Entamoeba hartmanni		-	Present	Present		-	-	-	-	-	-	-	-
Entamoeba sp.		Present	Present	Present		-	7/13	-	-	-	-	-	-
Iodamoeba butschlii		Present	Present	Present		-	4/13	-	in *E. coli*	-	-	26.7	-
Endolimax nana		Present	Present	Present		-	3/13	-	-	-	-	14.3	-
Chilomastix mesnili		-	-	-		-	-	-	in *E. coli*	-	-	-	-
Giardia sp.		-	Present	-		-	-	-	-	-	58	16	-
Dientamoeba fragilis		-	Present	Present		-	-	-	-	-	-	-	-
Toxoplasma gondii		-	-	-		-	-	-	-	-	-	-	-
Toxoplasma sp.		-	-	-		-	-	-	-	-	-	-	-
Sarcocystis sp.		-	-	-		-	-	-	-	-	-	-	-
Hepatocystis simiae		-	-	-		-	-	-	-	-	-	-	-
Trichomonas sp.		-	-	-		-	-	-	-	-	-	-	-
Cryptosporidium sp.		-	-	-		-	-	-	-	-	32	-	12
Eimeria sp.		-	-	-		-	-	-	-	-	99	-	-

FR=Forest Reserve; n/a = data non available

References: (1) Hahn *et al.* 2003, (2) Kuntz & Myers 1967, (3) Eley *et al.* 1989, (4) Munene *et al.* 1998, (5) Kuntz & Myers 1966, (6) McGrew *et al.* 1989, (7) Müller-Graf *et al.* 1996, (8) Murray *et al.* 2000, (9) Hope *et al.* 2004, (10) Ocaido *et al.* 2003, (11) Legesse & Erko 2004.

APPENDIX A continued

Helminths	*Papio cynocephalus* (yellow baboon)				*Papio hamadryas* (hamadryas baboon)						*Papio papio* (Guinea baboon)
	Kenya				Saudi Arabia						Senegal
	Hooks group (1)	Lodge group (1)	Amboseli (2)	Rift Valley Prov. (3)	Al-Baha (4)	Al-Taif (4)	Turabah (4)	Al-Rihat (4)	Al-Akhal (4)	Asir (5)	Niokolo Koba (6)
Nematoda											
Trichuris sp.	82	57	98	-	5	4	5	1	-	Present	28
Oesophagostomum sp.	29 **	13 **	26	34	-	-	-	-	-	-	-
Trichostrongylus sp.	-	-	81	17	-	-	-	-	-	-	-
Physaloptera sp.	67	7	37 / 88	2	-	-	-	-	-	-	31
Ascaris sp.	-	-	-	-	-	-	-	-	-	Present	-
Streptopharagus sp.	2	43	2	40	-	-	-	-	-	-	23
hookworm type	-	-	-	-	3	2	-	-	-	-	38
Spiruridae sp.	-	-	-	-	-	-	-	-	-	-	-
Ternidens deminutus	-	-	-	-	-	-	-	-	-	-	-
Strongyloides sp.	2	-	19	-	-	-	-	-	-	-	26
Enterobius sp.	-	-	-	43	1	3	1	1	-	Present	-
Cestoda											
Bertiella studeri	-	-	2	27	-	-	-	-	-	-	-
Taenia sp.	-	-	-	-	-	-	-	-	-	-	-
Hymenolepis sp.	-	-	-	-	8	9	2	2	-	Present	-
Trematoda											
Schistosoma sp.	-	-	-	-	4	-	-	-	-	-	23

(*) prevalence includes *Ternidens deminutus*, (**) prevalence includes all Strongylidis (*Oesophagostomum* sp., *Trichostrongylus* sp., *Ternidens* sp., etc.)

References: (1) Hahn *et al.* 2003, (2) Meade 1984, (3) Kuntz & Moore 1973, (4) Ghandour *et al.* 1995, (5) Nasher 1988, (6) McGrew *et al.* 1989

APPENDIX A continued

Protozoa	*Papio cynocephalus* (yellow baboon)				*Papio hamadryas* (hamadryas baboon)						*Papio papio* (Guinea baboon)
	Kenya				Saudi Arabia						Senegal
	Hooks group (1)	Lodge group (1)	Amboseli (2)	Rift Valley Prov. (3)	Al-Baha (4)	Al-Taif (4)	Turabah (4)	Al-Rihat (4)	Al-Akhal (4)	Asir (5)	Niokolo Koba (6)
Balantidium coli	n/a	n/a	n/a	75	6	3	3	-	-	-	72
Entamoeba coli				42	35	28	32	36	-	-	87
Entamoeba histolytica				16	25	20	17	25	-	Present	-
Entamoeba chattoni				7	-	-	-	-	-	-	-
Entamoeba hartmanni				28	-	-	-	-	-	-	-
Entamoeba sp.				-	-	-	-	-	-	-	-
Iodamoeba butschlii				28	-	-	-	-	-	-	38
Endolimax nana				9	-	-	-	-	-	-	-
Chilomastix mesnili				2	-	-	-	-	-	-	-
Giardia sp.				-	33	25	25	32	10	Present	-
Dientamoeba fragilis				-	-	-	-	-	-	-	-
Toxoplasma gondii				-	-	-	-	-	-	-	-
Toxoplasma sp.				-	-	-	-	-	-	-	-
Sarcocystis sp.				-	-	-	-	-	-	-	-
Hepatocystis simiae				-	-	-	-	-	-	-	-
Trichomonas sp.				-	-	-	-	-	-	-	-
Cryptosporidium sp.				-	-	-	-	-	-	-	-
Eimeria sp.				-	-	-	-	-	-	-	-

n/a = data non available

References: (1) Hahn *et al.* 2003, (2) Meade 1984, (3) Kuntz & Moore 1973, (4) Ghandour *et al.* 1995, (5) Nasher 1988, (6) McGrew *et al.* 1989

APPENDIX B: Statistical tests on collection time of faecal samples.

PSR: Kruskal-Wallis				
	n	U	df	p
Helminth PSR	50	8.926	9	0.444
Protozoan PSR	50	10.720	9	0.295
Parasite Presence/Absence Exact Chi-square				
	n	Chi-square	df	p
Trichuris sp.	50	10.939	9	0.263
Oesophagostomum sp.	50	13.666	9	0.122
Trichostrongylus sp.	50	6.295	9	0.752
Physaloptera sp.	50	10.106	9	0.408
Ascaris sp.	50	4.935	9	0.947
Hookworm type	50	7.483	9	0.697
Unidentified Spirurid	50	7.483	9	0.701
Balantidium coli	50	6.268	9	0.842
Entamoeba coli	50	7.483	9	0.706
E. histolytica/dispar	50	9.818	9	0.373
E. chattoni	50	5.970	9	0.788
E. hartmanni	50	3.034	9	0.973
Iodamoeba bütschlii	50	11.674	9	0.237
Chilomastix mesnili	50	4.719	9	0.911
Endolimax nana	50	7.742	9	0.530
Egg output log(x+1)-transformed: Kruskal-Wallis				
	n	U	df	p
Trichuris sp.	32	4.187	7	0.758
Oesophagostomum sp.	25	5.224	6	0.515

APPENDIX B continued: Statistical tests on collectors of faecal samples.

PSR: Kruskal-Wallis				
	n	U	df	p
Helminth PSR	50	0.002	1	0.963
Protozoan PSR	50	0.004	1	0.947

Parasite Presence/Absence Exact Chi-square				
	n	Chi-square	df	p
Trichuris sp.	50	1.472	1	0.414
Oesophagostomum sp.	50	1.814	1	0.295
Trichostrongylus sp.	50	0.19	1	1.000
Physaloptera sp.	50	2.367	1	0.186
Ascaris sp.	50	1.241	1	0.550
Hookworm type	50	0.397	1	1.000
Unidentified Spirurid	50	0.397	1	1.000
Balantidium coli	50	0.397	1	1.000
Entamoeba coli	50	0.397	1	1.000
E. histolytica/dispar	50	0.674	1	0.481
E. chattoni	50	0.105	1	1.000
E. hartmanni	50	0.651	1	0.533
Iodamoeba bütschlii	50	0.828	1	0.529
Chilomastix mesnili	50	0.674	1	0.481
Endolimax nana	50	0.045	1	1.000

APPENDIX C: Comparison of length and width of parasite eggs between troops. Spirurid and hookworm morpho-types were not analyzed, due to small sample size (n=13 and n=10 respectively).

Results of Kruskal-Wallis test

Parasite taxa	Length			Width		
	H	df	p	H	df	p
Oesophagostomum sp.	2.087	5	0.837	4.053	5	0.542
Trichostrongylus sp.	7.564	4	0.109	9.398	4	0.052
Ascaris sp.	11.9	4	**0.018**	37.478	4	**<0.001**
Physaloptera sp.	7.333	2	**0.026**	7.953	2	**0.019**

Results of post hoc tests (Mann-Whitney U-test). Troops: CP=Cape Point, DGP=Da Gama Park, KK=Kanonkop, PLT=Plateau Road, TK=Tokai.

1. *Ascaris* sp.

Troop	CP	DGP	KK	PLT	TK	
CP (*n*=20)		U=158.500 **p=0.007**	U=218.000 **p=0.003**	U=247.000 p=0.169	U=73.500 **p=0.006**	Width
DGP (*n*=29)	U=172.500 **p=0.017**		U=515.000 p=0.342	U=179.000 **p=0.000**	U=205.000 p=0.521	
KK (*n*=41)	U=379.000 p=0.633	U=364.000 **p=0.006**		U=200.500 **p=0.000**	U=327.000 p=0.986	
PLT (*n*=32)	U=254.000 p=0.214	U=382.500 p=0.239	U=502.500 p=0.088		U=50.500 **p=0.000**	
TK (*n*=16)	U=153.500 p=0.836	U=126.000 **p=0.012**	U=301.500 p=0.637	U=178.000 p=0.088		
	Length					

2. *Physaloptera* sp.

Troop	DGP	KK	PLT	
DGP (*n*=4)		U=0.000 **p=0.032**	U=28.500 p=0.070	Width
KK (*n*=3)	U=3.000 p=0.289		U=11.000 **p=0.025**	
PLT (*n*=31)	U=21.000 **p=0.032**	U=16.500 p=0.066		
	Length			

APPENDIX D: Ecology of gastrointestinal helminths and protozoa found in the chacma baboons of the Cape Peninsula (plus *Streptopharagus* sp. and *Strongyloides* sp.).

Parasite species	Life cycle	Infective stage	Routes of infection	Clinical symptoms in nonhuman primates	Potential of cross transmission with man	References
NEMATODES						
Trichuris cf. *trichiura* (whipworm)	Direct	Embryonated egg	Oral (soil)	Generally asymptomatic Heavy infections: diarrhoea, enteritis	Yes (9,4)	8, 3, 6
Oesophagostomum cf. *bifurcum*	Direct	L3, sheathed	Oral	Minor infections: no clinical signs Heavy infections: diarrhoea, weight loss, weakness, death	Yes (2,9) Reported (may be different strain) (4)	2, 8
Trichostrongylus cf. *falculatus colubriformis (2,4)*	Direct	L3, sheathed	Oral	Heavy infections: diarrhoea and eosinophilia Mild enteritis (4)	*T. colubriformis* Yes (2,9,4)	2, 8
Physaloptera caucasica	Indirect	Infected intermediate host insect (beetles, grasshoppers, cockroaches)	Ingestion intermediate host	Oesophagitis, gastritis, enteritis (4)	Yes (2,9,4)	2, 8
Ascaris cf. *lumbricoides*	Direct	Egg containing L2	Oral	Not reported (2) Hepatic abscesses (4)	Yes (2,9,4)	2, 8
Hookworm	Direct	L3, filariform, sheathed	Skin, Oral	Unknown (2) Anaemia (4)	Yes (2,9,4)	2, 8
Streptopharagus pigmentatus	Indirect	Intermediate host (arthropods)	Oral	Unknown (4)	Not reported (4)	8
Strongyloides fuelleborni	Direct or Indirect	L2	Skin, Oral	Heavy infections: diarrhoea	Yes (2,9,4)	2, 8
Strongyloides stercoralis	Direct or Indirect	L2	Skin, Oral	Heavy infections: acute catarrhal to haemorrhagic diarrhoea	Yes (2,9,4)	2, 8, 6

References: (1) Audebert *et al*. 2003, (2) Brack 1987, (3) CDC [http://www.dpd.cdc.gov/dpdx], (4) Cogswell 2007, (5) Feachem *et al.* 1983, (6) FELASA 1999, (7) Goldsmid & Rogers 1978, (8) Meade 1984, (9) Taylor 2001, (10) WHO 1994, 2004.

APPENDIX D continued

Parasite species	Life cycle	Infective stage	Routes of infection	Clinical symptoms in nonhuman primates	Potential of cross transmission with man	References
PROTOZOA						
Balantidium coli	Direct	Cyst	Oral	Usually asymptomatic Occasionally soft faeces	Yes (2,9,4)	2
Entamoeba coli	Direct	Cyst	Oral	Non-pathogenic	Yes (4)	10
E. histolytica /dispar (morphologically identical)	Direct	Cyst	Oral	*E. histolytica*: enteritis, hepatitis (4) *E. dispar*: Non-pathogenic	*E. hist.* Yes (2,9,4)	10
E. chattoni	Direct	Cyst	Oral	Usually no clinical signs (2,4)	Yes (2,9,4)	2
E. hartmanni	Direct	Cyst	Oral	Non-pathogenic	Yes (4)	10
Iodamoeba buetschlii	Direct	Cyst	Oral	Non-pathogenic	Yes (4)	10
Endolimax nana	Direct	Cyst	Oral	Non-pathogenic	Yes (4)	10
Chilomastix mesnili	Direct	Cyst	Oral	Non-pathogenic	Yes (4)	10

References: (1) Audebert *et al*. 2003, (2) Brack 1987, (3) CDC [http://www.dpd.cdc.gov/dpdx], (4) Cogswell 2007, (5) Feachem *et al.* 1983, (6) FELASA 1999, (7) Goldsmid & Rogers 1978, (8) Meade 1984, (9) Taylor 2001, (10) WHO 1994, 2004.

APPENDIX D continued

Parasite species	Stage excreted	Size in µm	Time to infective stage	Resistance of infective stage	Pre-patent period	Life span of adult parasite	References
NEMATODES							
Trichuris cf. *trichiura*	Eggs	54-62x26-31 (8)	Embryonation in 15-30 days	Eggs resistant to harsh climatic conditions for few months	60-70 days	Ca. 1-3 years	8, 3
Oesophagostomum cf. *bifurcum*	Eggs	48-72x27-55 (2) 82x44-54 (8) ~55-74x37-50 (7)	L1 can hatch in 24-48 hrs L1-L3 in 6-7 days	L1, L2 v sensitive to drying L3 may live for several months under favourable conditions	(more than 5-8 days) (2)	1-2 to few years	2, 8
Trichostrongylus cf. *falculatus colubriformis (2,4)*	Eggs	79-101x34-47 (2) 82-89x41-47 (8) ~80-93x37-43 (7)	L1 in 19 hrs (18 to 21°C) L3 65 to 68 hrs later (at 27°C)	L1, L2 v sensitive to drying Eggs and L3 very resistant especially at lower T	(more than 6-10 days) (2) 16-17 days in rabbit (1)	Unknown	2, 8
Physaloptera caucasica	Eggs	28-57x18-39 (8) ~63-77x48-58 (7)	Unknown (2)	Unknown (4)	Unknown (4)	Unknown	2, 8
Ascaris cf. *lumbricoides*	Eggs	65-75x35-50 (2)	Embryonation in 2-4 weeks L1 in egg 9-13 days (22 to 33°C), still in egg L1 to L2 in egg in 1 week Ref 3: 18 days to several weeks	Eggs can survive several months to 1 year, can survive putrefaction and desiccation; only moderately resistant to cold Optimum: moist, warm, shaded soil (ref 3)	2-3 months (2, 3)	1-2 years (ref 3)	2, 8
Hookworm	Eggs	60x40 (2) 56-60x36-40 (8)	L1 in 24-48 hrs in moist, shaded envir. (25°C) L1 to L2 in 2-3 days L2 to L3 in few days	L1, L2 can feed L3 can survive for 2-3 months in soil L1 might migrate beneath the surface of the soil	4-7 weeks (2)	1-2 to several years (3)	2, 8, 3
Streptopharagus pigmentatus	Eggs	~30-42x17-28 (7)	Unknown	Unknown	Unknown	Unknown	8
Strongyloides fuelleborni	Eggs	Rhabditiform larva: 150-390 (2)	L2 in 20-30 hrs (direct cycle)	Weeks, in soil	11-18 days (2)	Unknown	2, 8
Strongyloides stercoralis	L1	Rhabditiform larva: 150-390 (2)	L2 in 20-30 hrs (direct cycle)	Weeks, in soil	11-18 days (2)	Unknown	2, 8

References: (1) Audebert *et al*. 2003, (2) Brack 1987, (3) CDC [http://www.dpd.cdc.gov/dpdx], (4) Cogswell 2007, (5) Feachem *et al.* 1983, (6) FELASA 1999, (7) Goldsmid & Rogers 1978, (8) Meade 1984, (9) Taylor 2001, (10) WHO 1994, 2004.

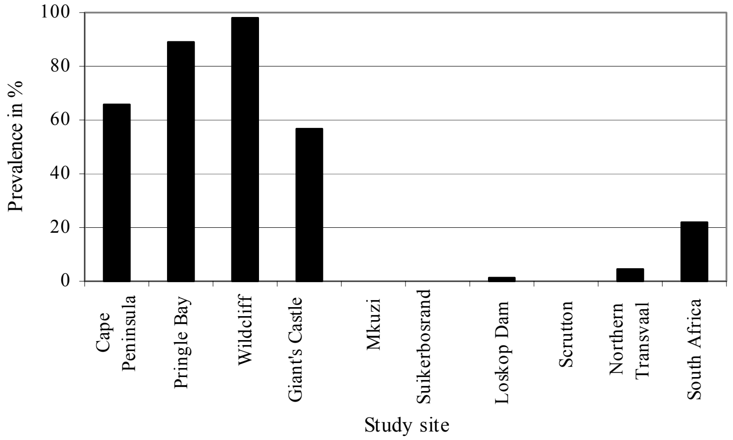
APPENDIX D continued

Parasite species	Stage excreted	Size in µm	Time to infective stage	Resistance of infective stage	Pre-patent period	Life span of adult parasite	References
PROTOZOA							
Balantidium coli	Cysts/ trophozoites (in diarrhoeal faeces)	50-70	0	Cysts can survive several weeks in moist envir at 22°C, but sensitive to drying and sunlight	Short	n/a	2, 10
Entamoeba coli	Cysts	15-30	0	Ca. 10 days in soil. Susceptible to desiccation and freezing (5)	Short	n/a	10
E. histolytica /dispar	Cysts/ trophozoites (in diarrhoeal faeces)	10-20	0	Cysts very resistant to low temperatures. Can survive weeks to months in moist environment. Resistant to chemical disinfectants. Susceptible to drying, UV-light.	Short	n/a	10
E. chattoni	Cysts	9-18	0	Ca. 10 days in soil. Susceptible to desiccation and freezing (5)	Short	n/a	2, 10
E. hartmanni	Cysts	5-10	0	Ca. 10 days in soil. Susceptible to desiccation and freezing (5)	Short	n/a	10
Iodamoeba buetschlii	Cysts	5-20	0	n/a	Short	n/a	10
Endolimax nana	Cysts	5-10	0	n/a	Short	n/a	10
Chilomastix mesnili	Cysts	6-10	0	n/a	Short	n/a	10

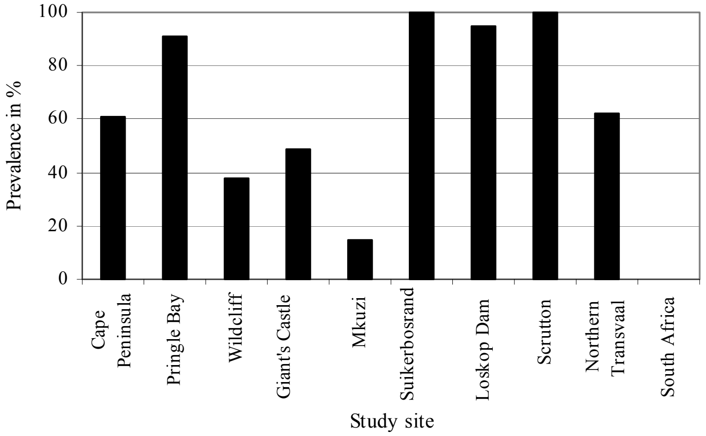
References: (1) Audebert *et al*. 2003, (2) Brack 1987, (3) CDC [http://www.dpd.cdc.gov/dpdx], (4) Cogswell 2007, (5) Feachem *et al.* 1983, (6) FELASA 1999, (7) Goldsmid & Rogers 1978, (8) Meade 1984, (9) Taylor 2001, (10) WHO 1994, 2004.

APPENDIX E: The prevalence of gastrointestinal parasite infections in chacma baboons in various locations in South Africa.

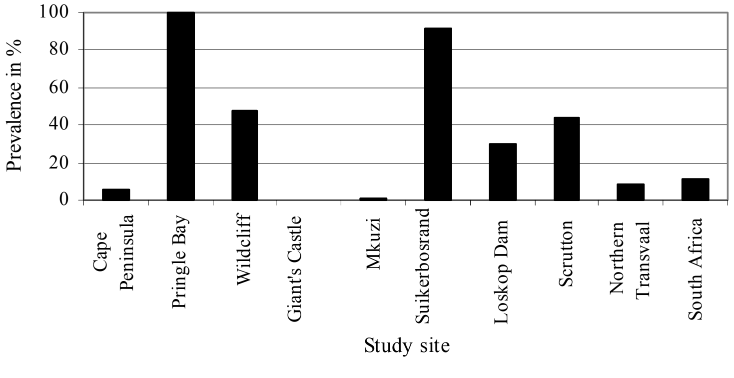
Trichuris sp.



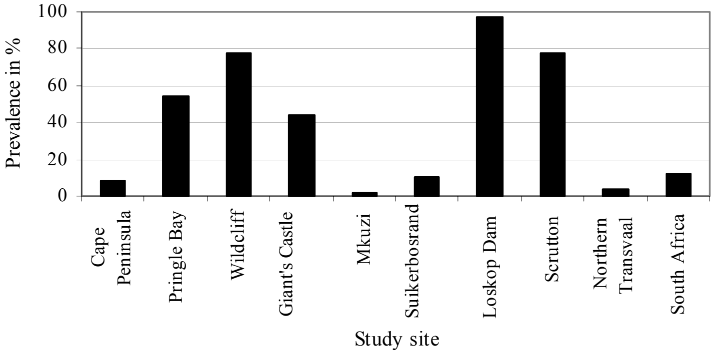
Oesophagostomum sp.

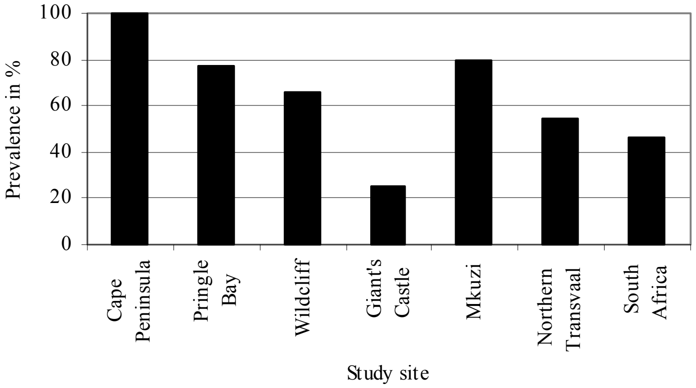


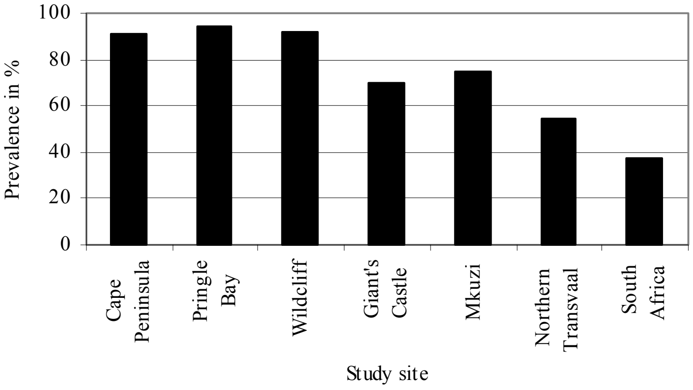
Trichostrongylus sp.



APPENDIX E continued

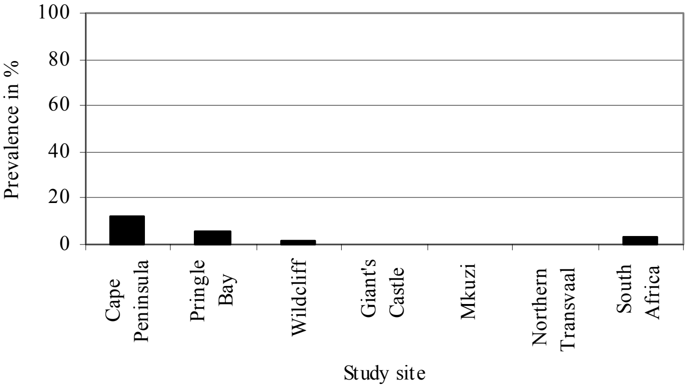

Physaloptera sp.


Balantidium coli

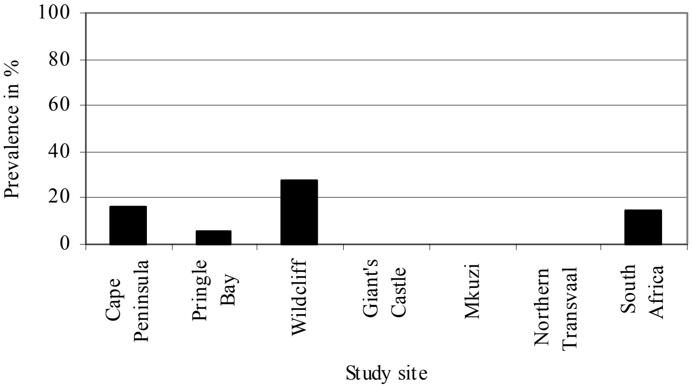

Entamoeba coli

APPENDIX E continued

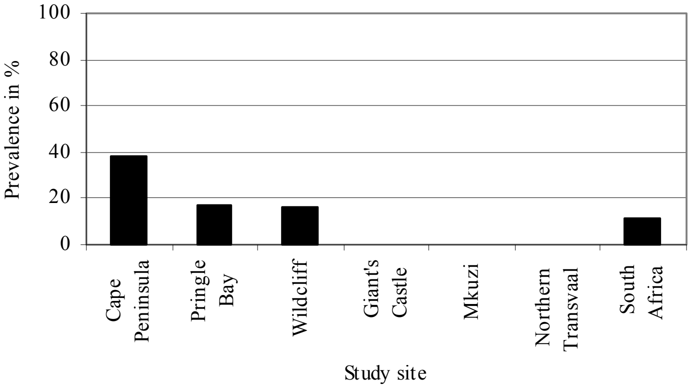
Entamoeba histolytica



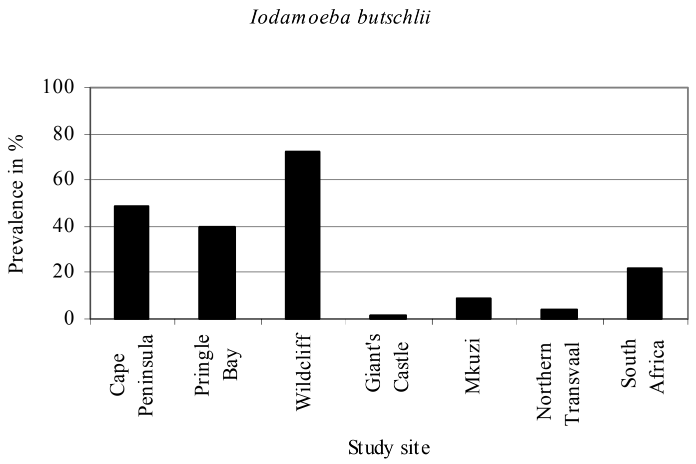
Entamoeba chattoni

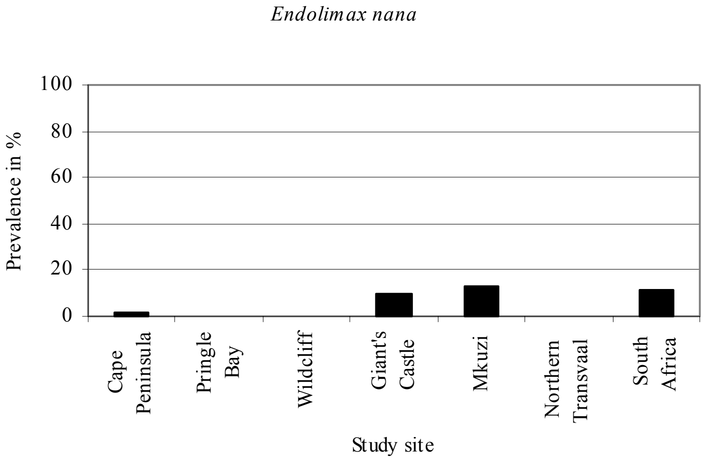


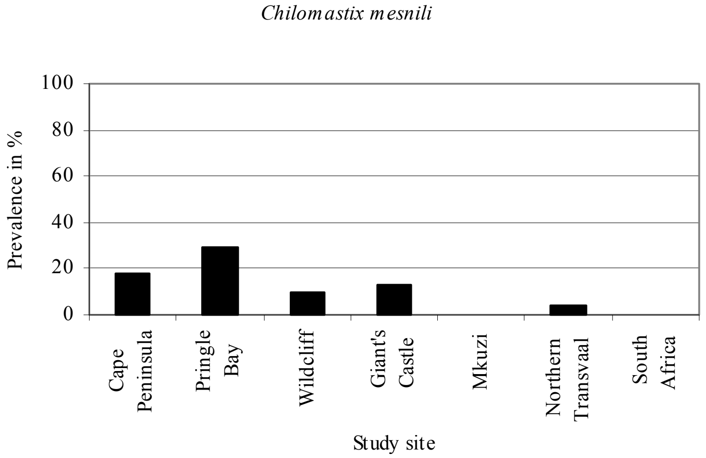
Entamoeba hartmanni



APPENDIX E continued







APPENDIX F: Comparison of prevalences of parasite taxa between each troop. Results of Mann-Whitney U-test (n.s.=not significant) BB=Buffels Bay, CP=Cape Point, KK=Kanonkop, PLT=Plateau Road, DGP=Da Gama Park, TK=Tokai. Bold: significant after implementing false discovery rate control (Narum 2006).

Troop	BB	CP	KK	PLT	DGP	TK	
BB		U=294 p=0.021	n.s.	n.s.	U=592 p=0.007	U=308 p=0.018	*Physaloptera sp.*
CP	n.s.		n.s.	n.s.	n.s.	n.s.	
KK	U=1062 p=0.023	n.s.		n.s.	n.s.	n.s.	
PLT	n.s.	n.s.	n.s.		n.s.	n.s.	
DGP	n.s.	n.s.	n.s.	n.s.		n.s.	
TK	U=324 p=0.009	n.s.	n.s.	n.s.	n.s.		
	Ascaris sp.						

Troop	BB	CP	KK	PLT	DGP	TK	
BB		n.s.	n.s.	n.s.	U=551 **p=0.002**	U=236 **p=0.003**	*Trichuris sp.*
CP	n.s.		U=519 p=0.019	n.s.	U=216 **p<0.001**	n.s.	
KK	n.s.	n.s.		n.s.	U=1080 **p=0.002**	U=425 **p<0.001**	
PLT	n.s.	n.s.	n.s.		U=1231 **p<0.001**	U=566 **p=0.001**	
DGP	n.s.	n.s.	n.s.	n.s.		U=155 **p<0.001**	
TK	n.s.	n.s.	n.s.	n.s.	n.s.		
	Trichostrongylus sp.						

Troop	BB	CP	KK	PLT	DGP	TK	
BB		n.s.	U=900 **p=0.006**	n.s.	U=423 **p<0.001**	n.s.	*Oesophagostomum sp.*
CP	n.s.		U=440 **p=0.001**	n.s.	U=196 **p<0.001**	n.s.	
KK	n.s.	n.s.		U=2398 p=0.049	U=1168 p=0.031	U=516 **p=0.007**	
PLT	n.s.	n.s.	n.s.		U=1170 **p<0.001**	n.s.	
DGP	n.s.	n.s.	n.s.	n.s.		U=238 **p<0.001**	
TK	n.s.	n.s.	n.s.	n.s.	n.s.		
	Hookworm type and Spirurid						

APPENDIX F continued

Troop	BB	CP	KK	PLT	DGP	TK	
BB		U=317 p=0.038	U=1060 p=0.043	U=1284 p=0.034	n.s.	n.s.	*Entamoeba histolytica/dispar*
CP	n.s.		n.s.	n.s.	n.s.	n.s.	
KK	n.s.	n.s.		n.s.	n.s.	n.s.	
PLT	n.s.	n.s.	n.s.		n.s.	n.s.	
DGP	U=587 p=0.018	n.s.	U=1107 **p=0.010**	n.s.		n.s.	
TK	U=304 p=0.030	n.s.	U=573 p=0.023	n.s.	n.s.		
	Entamoeba chattoni						

Troop	BB	CP	KK	PLT	DGP	TK	
BB		n.s.	n.s.	n.s.	U=631 p=0.049	n.s.	*Chilomastix mesnili*
CP	n.s.		n.s.	n.s.	n.s.	n.s.	
KK	n.s.	n.s.		n.s.	n.s.	n.s.	
PLT	n.s.	U=830 p=0.047	n.s.		U=1313 **p=0.003**	n.s.	
DGP	n.s.	n.s.	n.s.	n.s.		n.s.	
TK	n.s.	n.s.	n.s.	n.s.	n.s.		
	Endolimax nana						

Troop	BB	CP	KK	PLT	DGP	TK	
BB		n.s.	n.s.	n.s.	n.s.	n.s.	*Balantidium coli*
CP	n.s.		n.s.	n.s.	n.s.	n.s.	
KK	n.s.	n.s.		n.s.	n.s.	n.s.	
PLT	n.s.	U=725 p=0.044	n.s.		n.s.	n.s.	
DGP	n.s.	n.s.	n.s.	n.s.		n.s.	
TK	n.s.	n.s.	n.s.	n.s.	n.s.		
	Entamoeba coli						

Troop	BB	CP	KK	PLT	DGP	TK	
BB		n.s.	n.s.	n.s.	n.s.	U=219 **p=0.001**	*Iodamoeba bütschlii*
CP	n.s.		n.s.	n.s.	n.s.	U=109 **p<0.001**	
KK	n.s.	n.s.		n.s.	n.s.	U=388 **p<0.001**	
PLT	U=1089 **p=0.003**	n.s.	U=2057 **p=0.001**		n.s.	U=587 **p=0.003**	
DGP	n.s.	n.s.	n.s.	U=1137 **p<0.001**		U=304 **p=0.010**	
TK	U=216 **p<0.001**	U=143 **p=0.003**	U=408 **p<0.001**	n.s.	U=219 **p<0.001**		
	Entamoeba hartmanni						

APPENDIX G: Correlations between independent troop variables; Spearman's Rank Correlation, *n*=6. HR=home range, Transf.=transformed land. Bold: significant after implementing false discovery rate control (Narum 2006).

		Group size	Host density	HR Size	HR Use Intensity	No. Overlap Troops	HR Overlap Troops	HR Overlap Urban	HR Overlap Transf.	Monitors Presence	No. Sleep Sites	Prop. Human Food	Rainfall
Group size	r_s		0.429	0.714	-0.714	-0.383	-0.866	-0.086	0.371	0.098	0.943	-0.833	0.577
	p		0.198	0.055	0.055	0.227	**0.009**	0.436	0.234	0.427	**0.002**	0.020	0.115
Host density	r_s			-0.029	0.029	-0.971	-0.600	0.257	0.943	0.488	0.371	0.000	0.880
	p			0.479	0.479	**≤0.001**	0.104	0.311	**0.002**	0.163	0.234	0.500	**0.010**
HR Size	r_s				-1.000	0.000	-0.371	0.086	-0.086	0.098	0.829	-0.617	0.334
	p				**<0.001**	0.500	0.234	0.436	0.436	0.427	0.021	0.096	0.259
HR Use Intensity	r_s					0.000	0.371	-0.086	0.086	-0.098	-0.829	0.617	-0.334
	p					0.500	0.234	0.436	0.436	0.427	0.021	0.096	0.259
No. Overlap Troops	r_s						0.471	-0.441	-0.971	-0.503	-0.383	-0.079	-0.938
	p						0.173	0.190	**<0.001**	0.155	0.227	0.441	**0.003**
HR Overlap Troops	r_s							0.314	-0.486	-0.098	-0.714	0.741	-0.516
	p							0.272	0.164	0.427	0.055	0.046	0.147
HR Overlap Urban	r_s								0.314	0.683	0.200	0.525	0.516
	p								0.272	0.067	0.352	0.143	0.147
HR Overlap Transf.	r_s									0.293	0.314	0.000	0.880
	p									0.287	0.272	0.500	**0.010**
Monitors Presence	r_s										0.293	0.422	0.518
	p										0.287	0.203	0.146
No. Sleep Sites	r_s											-0.679	0.638
	p											0.069	0.087
Proportion Human Food	r_s												-0.098
	p												0.426
Rainfall	r_s												
	p												

HR=Home range; Transf.=transformed land

APPENDIX H: Correlations between nematode prevalences; Spearman's Rank Correlation, *n*=6. (*Oesoph.*=*Oesophagostomum*, *Trichostr.*=*Trichostrongylus*). Bold: significant after implementing false discovery rate control (Narum 2006).

		Trichuris sp.	*Oesoph.* sp.	*Trichostr.* sp.	*Ascaris* sp.	Hookworm	Spirurid
Trichuris sp.	r_s		0.886	0.429	-0.371	0.541	0.393
	p		**0.009**	0.198	0.234	0.134	0.221
Oesoph. sp.	r_s			0.086	-0.200	0.304	0.393
	p			0.436	0.352	0.279	0.221
Trichostr. sp.	r_s				-0.029	0.034	0.655
	p				0.479	0.475	0.079
Ascaris sp.	r_s					-0.676	0.393
	p					0.070	0.221
Hookworm	r_s						-0.310
	p						0.275
Spirurid	r_s						
	p						