An Assessment of Primate Health in the Sabangau Peat-Swamp Forest, Central Kalimantan, Indonesian Borneo





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So, naturalists observe, a flea has smaller fleas that on him prey; and these have smaller still to bite 'em; and so proceed *ad infinitum*.

- Jonathan Swift



Abstract

The peat-swamp forests of Indonesian Borneo represent a biologically diverse and unique ecosystem, yet remain relatively understudied. There is a paucity of published literature on red langurs (Presbytis rubicunda) and nothing is known of factors affecting inter-specific parasite transmission and disease spread between other primate species. Utilising sodium-nitrate floatation methods to recover gastro-intestinal parasites, health of a primate community was assessed using parasitism as a proxy. Parasites may be substantial determinants of host-health and may show significant influence on survival and reproduction of populations. Hosts are typically parasitized with multiple parasite taxa which may be shared between sympatric species within the region, emphasising the importance of understanding the cumulative effects of co-infection on certain host traits. As part of a comprehensive ecological survey of P. rubicunda, baseline parasitological data were provided for sympatric primate species Bornean orangutans (Pongo pygmaeus) and Bornean agile gibbons (Hylobates albibarbis) inhabiting the Sabangau forest in Kalimantan, Indonesian Borneo in order to monitor changes in susceptibility and the dynamics of emerging infectious disease. Parasitism was measured in terms of prevalence, parasitic output, richness and multiple species infections. Within all primate species a rich diversity of parasite taxa were identified. Protozoa recovered included Entamoeba coli, Entamoeba histolytica/dispar, Balantidium coli, Blastocystis hominis and a symbiotic ciliate involved in cellulose digestion Troglodytella abrassarti. Helminths recovered included Strongyloides sp., Trichostrongylus sp., Trichuris trichuria, Enterobius vermicularis, Ascaris lumbricoides, Schistosoma mansoni and hookworms. Primates exhibiting the greatest similarities in socioecological factors and exhibiting overlap in niche occupancy had greatest similarities in parasite infections. Langurs had a higher parasitic prevalence than both orangutans and gibbons. Host density and dietary composition were identified as likely determinants of parasite infections, in support of previous findings. Greater incorporation of parasitic research into conservation and monitoring programs will maximise information obtained from ecosystem-based studies.

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List of Abbreviations

AIDS:	Acquired Immunodeficiency Syndrome
CIMTROP:	Centre for International Co-operation in Management of Tropical Peat-lands
EID:	Emerging Infectious Disease
ESU:	Evolutionary Significant Unit
GPS:	Global Positioning System
На	Hectare
HIV:	Human-Immunodeficiency Virus
IUCN:	International Union for Conservation of Nature
LAHG:	(Laboratorium Alam Hutan Gambut) - Natural Laboratory of Peat-Swamp Forest
NHP:	Non-Human Primate
OUTROP:	Orangutan Tropical Peatland Project
PSF:	Peat-Swamp Forest
PSR:	Parasite Species Richness
RISTEK:	(<i>Kementerian Riset dan Teknologi</i>) – Indonesian Research Ministry
SSC:	Species Survival Commission
UNPAR:	University of Palangka Raya

Chapter One – General Introduction

The role that parasitism plays in the behavioural ecology and evolution of primates remains largely unappreciated and is often overlooked in ecosystem survey efforts (Nunn & Altizer 2006; Huffman & Chapman 2009). However, although often cryptic the effects of parasitism in all ecological interactions are an integral facet of ecosystem function and may even guide the evolution of primate sociality and behaviour (Freeland 1976, 1980). Investigations into the diversity of parasites and the spread of disease provide powerful insights into ecosystem structure and the biogeography of other organisms, and inform about threats to endangered species (Poulin & Morand 2000; Daszak 2001; Cleaveland et al. 2002; Lafferty & Holt 2003).

The aim of this study is to gauge status of health of the primate species living within a tropical peat-swamp forest (PSF) in order to assess trends in spread of disease, as an integrated aspect of ecosystem monitoring and for informing conservation management. One of the most powerful methods for dissemination of this information is by the examination of faeces for gastro-intestinal parasites (Stuart & Strier 1995; Dryden et al. 2005; Gillespie 2006). By investigating a range of host-intrinsic factors including age and sex of the host, group size and density, home range, nutritional status, use of strata and dietary composition sympatric primate species may be compared with one another in terms of parasite prevalence and diversity (Nunn & Altizer 2006; Müller 2007; Huffman & Chapman 2009). Causal determinants of parasite levels may be identified and related to the degree of niche overlap in the host.

Parasites may be important determinants of host-health and show significant influence on survival and reproduction of populations (Scott 1988; Lewis et al. 2002; Roberts & Janovy 2008). On an individual level parasite burdens can have relatively low impact, but with greater infection intensity and ensuing immunosuppression nutritional intake may be compromised influencing ecological processes (Coop & Holmes 1996; Behnke 1990). More intensive parasitosis can cause significant physical impairment to an individual, and subsequently reduce population health leading to disease outbreaks and epidemics that may result in inter-specific transmission across species (Behnke 1990; Despommier et al. 1995; Ezenwa 2003). Therefore, parasites may act as useful indicators for the health of individuals and provide valuable insight into the condition of the population and the threats that it faces. Identifying the factors that influence distribution of infective agents is not only important for wildlife conservation but also for human health (Soulsby 1974; Daszak et al. 2000; Goldberg et al. 2008; Rwego 2009; Shakespeare 2009) which is discussed shortly.

A considerable number of investigations describe the parasitological communities of primates (see Nunn et al. 2003 for a comprehensive review). The tropical rainforests of Indonesia have been the site for a number of these studies (Collet et al. 1986; Warren et al. 1998; Jones-Engel et al. 2004; Mul et al. 2007; Labes et al. 2010), although there remains a substantial gap in our sampling efforts in research efforts in particular regions such as Kalimantan (Hopkins & Nunn 2007; Gillespie et al. 2008). No published research examining the parasite communities of Bornean red langurs (*Presbytis rubicunda*) or Bornean agile gibbons (*Hylobates albibarbis*) exist and virtually nothing is known about the behavioural ecology of langur populations living in PSF. However, there are a reasonable amount of data representing parasitism of other colobines (Munene et al. 1998; Chapman et al. 2005a, b; Gillespie et al. 2006) and orangutans (Collet et al. 1986; Foitová 2002; Kilbourn et al. 2003; Foitová et al. 2009; Labes et al. 2010) which may provide valuable comparisons for transmission trends and geographic variation in parasite spread.

As part of a comprehensive ecological survey of *P. rubicunda* inhabiting the Sabangau forest catchment in Kalimantan, Indonesian Borneo, baseline parasitological data were provided for these arboreal colobines. Sympatric primate species Bornean orangutans (*Pongo pygmaeus*) and Bornean agile gibbons (*H. albibarbis*) were also examined in order to monitor changes in susceptibility and identify key traits of the primate host that may affect parasite transmission. With this research I aim to highlight the importance of baseline patterns of parasitism for monitoring wildlife and ecosystem health. Furthermore I hope to contribute to our knowledge of the directional associations between primate socioecology and parasitism.

1.1 Dissertation Format

I have written this dissertation in a format that includes two chapters suitable for journal article publication. I recognise that the data and subsequent discussion are of sufficiently high quality and contribute to our knowledge of primate socioecology and parasitology as well as our understanding of ecosystem health for informing management decisions for conservation purposes. I have based my experimental design and the formulation of my research on answering two central questions as outlined below:

1. What is the importance of monitoring primate population health?

2. Which socioecological variables are likely to play key roles in governing the parasite communities of primates?

In addition to these principal questions driving the direction of the research and forming the basis of the articles, there are three other key questions that I have identified from a broad literature search that relate this topic to conservation measures:

- 1. How can parasitism be utilised in monitoring of primate population health?
- 2. How does living in sympatry affect the spread of gastro-intestinal parasites and what does this mean for disease transmission dynamics?
- 3. What can be contributed to primate conservation management by incorporating parasite surveillance into bio-monitoring programs?

These questions are fundamental elements of epidemiological research, and providing data that can support previous theories can substantially aid our understanding of disease spread and the factors responsible.

I have developed the first article (Chapter 3) for submission to the well-regarded journal Biotropica which presents original research on ecology, conservation and management of tropical ecosystems. This paper provides an authoritative commentary on what is an ongoing discussion of health indices and infectious disease monitoring across the whole ecosystem (e.g Krief et al. 2005; Gillespie 2006; Deem et al. 2008; Petrášová et al. 2010). I have taken an ambitious approach to the subject, putting forward a synthesis of current thinking on health monitoring, with primates and parasite surveillance as a prominent case, placing the remainder of my thesis in context.

The second article (Chapter 4) takes a socioecological approach, elucidating how overlap in ecological niches between sympatric primates may affect parasite diversity and prevalence. A notable contribution to our knowledge and understanding of the diversity of the parasites infecting primates has been made to the American Journal of Primatology. The data I present fit into the remit of the journal and provide input to an understudied element of transmission dynamics, expanding on research by other primate parasitologists such as Colin Chapman, Thomas Gillespie, Michael Huffman and Charles Nunn whom have contributed several pertinent additions on primates and the ecology of infectious disease (e.g Chapman et al. 2005a, b; Gillespie et al. 2005a, b; Nunn & Altizer 2006; Huffman & Chapman 2009). Both of these chapters adhere to author guidelines as laid out by the respective journal.

In the following section I introduce parasitism, drawing focus on the ecological importance of parasites and their integral role in ecosystem function, whilst highlighting the complexities of parasite-host relationships within a primatological context.

1.2 Parasite Diversity

If one applies a broad definition, it is recognised that most of the extant species on the planet are parasitic (Price 1980; Windsor 1998; Thomas et al. 2009). Furthermore, practically all free-living organisms including many parasites themselves have their own parasites (Bush 2001). Parasites are highly specialised organisms that have evolved over millions of years to exploit their environment which constitutes the bodies of other organisms (Poulin & Morand 2005; Ryan & Ray 2010). A great diversity of parasites exists representing numerous phyla. Presence of parasites from at least one member of the host population reflects infection with either a macroparasite (helminth or arthropod, commonly referred to as 'metazoa') or microparasite (bacteria, virus or protozoa). Most coprological assessments recover a community of protozoa and metazoan that represent basic parasitic gut fauna (Bush et al. 1997; WHO 2004; Dryden et al. 2005). The helminths, including the

most speciose of all phylum Nematoda (roundworms) commonly occur in primate parasite surveys (Nunn & Altizer 2005) and constitute at a very minimum 10,500 parasitic species (Blaxter et al. 1998; Anderson & Anderson 2000) with some estimates as high as almost 16,000 species (Hugot et al. 2001).

The study of gastro-intestinal parasites can yield a substantial wealth of information about an individual host and point to characteristics of the population (Bush 2001). Hosts usually harbour several different species of parasite consecutively, making use of niche space within organ tissues (Holmes & Price 1986; Keeney & Poulin 2007). These multiple species infections constitute co-infective communities which may interact with one another in different ways dependent on their ecological and reproductive mechanisms (Esch et al. 1990; Poulin 1997; Nunn et al. 2003). This community presence and the subsequent use of the host's internal resources is an important factor that may also contribute to the diversity and types of parasites present within the environment (Poulin 1997; Keeney & Poulin 2007).

1.2.1 Parasite Host Specificity

Categories may be given to parasites based on host specificity, which refers to the spectrum of host species that a parasite can exploit at a particular stage of its life cycle. Specialist parasites are those that infect a single host, whilst generalist parasites are those that are capable of occupying multiple host species (Scott 1988). Generalists are the most commonly occurring parasites, representing over two thirds of parasites identified in primates (Pederson et al. 2005) and being responsible for the majority of severe, parasite-induced declines in primate populations (Walsh et al. 2003; Gillespie & Chapman 2008).

The addition of new hosts to existing host–parasite systems can have major consequences for disease spread and evolution (Woolhouse et al. 2001; Gandon 2002; Holt et al. 2003). Furthermore, around 60% of all infectious organisms that are known to infect humans are zoonotic (transmittable from animals to humans) (Taylor et al. 2001; Shakespeare 2009), thus illustrating the importance of understanding the distribution of these multi-host pathogens for both wildlife conservation and human health management (Daszak 2000; Cleaveland et al. 2002; Michaud et al. 2003).

1.2.2 Modes of Transmission

A broad spectrum of transmission strategies exists across different disease causing pathogens (Woolhouse et al. 2001; Lewis et al. 2002; Pederson et al. 2005). These vary from direct transmission through close contact, environmental transmission or reliance on vectors or intermediate hosts as part of the life cycle and transitory stages of infection (Nunn & Altizer 2006). The majority of gastro-intestinal parasites, including those examined in this study, incorporate several strategies such as free-living stages in the environment by *Strongyloides* sp., (Ryan & Ray 2010) or intermediate arthropod hosts such as with the trematode *Schistosoma mansoni* utilising a secondary host snail species for cercariae transmission (Sadun et al. 1966; Boissier et al. 1999). Vector transmission is more common among protozoa whilst intermediate hosts occur more frequently within the helminth clade (Roberts & Janovy 2008).

It should be kept in mind that while we can make inferences regarding impacts of transmission routes and potential facilitation of infectious disease, many other parasites may be acting simultaneously with markedly different strategies further adding to the complexity of parasite community assemblages (Lewis et al. 2002). Determination of transmission route may be a substantial challenge as it may require rigorous experimental manipulation, but is a necessary consideration with regards to primate epidemiology for several reasons. Firstly, contact rate is likely to increase parasite prevalence and diversity of primate assemblages (Anderson & May 1979; Mbora & McPeek 2009), thus exacerbating spread of parasites between social animals. Primates are highly social, gregarious mammals and subsequently stand higher probability of increased direct transmission (Ezenwa 2003). This reason, combined with our close phylogenetic similarities that create ideal conditions for potential cross-transmission identify primates as important candidates for epidemiological research (Contacos 1970; Behnke 1990; WHO 2004; Ekanayake et al. 2006; Nunn & Altizer 2006; Chapman et al. 2007; Shakespeare 2009).

1.3 Parasite-host Relationships

A plethora of complex interactions occur between parasites and their hosts (Bush 2001; Lafferty & Holt 2003; Vitone et al. 2004; Müller 2007). Understanding the cumulative effects of co-infection on certain host traits is therefore integral to understanding how these relationships affect the health of individuals and populations. These traits may be divided into those directly related to the host (host-intrinsic factors) and those which externally impact host survival and the conditions which the primate species are subjected to (hostextrinsic factors).

1.3.1 Host-Intrinsic Factors

Primates are subjected to a wide range of socioecological factors that influence the potential for parasite establishment and spread in numerous ways (Hausfater & Meade 1982; Nunn & Altizer 2006; Huffman & Chapman 2009). These factors may be directly related to the individual host, the group or population of potential hosts, the environment in which parasites may be spread and the biology and transmission strategies of the particular parasites themselves (Arneberg et al. 1998). Key individual host traits include body size, sex, age, social dominance and reproductive status. On a group or population level, group size, host density, social and mating systems, strata use, diet, nutritional status and ranging behaviour have all been shown to influence parasite infections (see Nunn & Altizer 2006 for a broad overview of these interactions).

Host density has been shown to have a major impact on the prevalence and PSR in primates (Arneberg 2002; Mbora & McPeek 2009). Additionally, body size is a major component of social organisation widely viewed as increasing disease risk in primates (Freeland 1976; Nunn & Heymann 2005) and has been shown to correlate with parasitic output and PSR (Nunn et al. 2003). However, it has strong links to group size which has been proposed as a better estimate of potential parasite habitat (Nunn & Altizer 2006). Other demographic variables such as range are also important considerations for encounter probability (Hausfater & Meade 1982; Nunn & Dokey 2006). Nutritional intake of the host can affect its susceptibility to infection (Moore 2002; Roberts & Janovy 2008), with dietary

composition another indicator of health likely to vary between primate species. This and other evidence from previous research identifies factors most likely to play a key role in parasite prevalence and PSR as host body size, density, range, group size and diet. I will therefore focus on these variables whilst briefly considering the other factors for this study, with an investigation into these socioecological determinants for three primate hosts presented in Chapter 4.

1.3.2 Host-Extrinsic Factors

In addition to the variety of host characteristics as described above, the potential for parasites to spread across hosts may also be influenced by qualities of the external environment, known as host-extrinsic factors. These constitute aspects of the habitat that the host depends on, predominantly the distribution of resources available. However, the type of vegetation, amount of solar radiation, distribution of intermediate hosts, ground morphology, soil PH and amount of leaf litter are amongst a plethora of different characteristics that constitute the arena for the transfer between parasites and hosts (Lewis et al. 2002; Mitchell et al. 2005; Wolinska & King 2009).

Figure 1 illustrates these key factors of parasite-host interactions and their inter-relation with one another with regards to parasite spread. Without baseline data of the parasite assemblages of hosts involved in these processes, we are unable to monitor fluctuations in susceptibility and potential health deficits. As so little is known about parasite and disease transmission in this region and under these conditions, emergence of infectious disease could be capable of having substantial impact on a population potentially escalating the risks of local extinction.



Figure 1. Schematic diagram representing the interactions between socioecological factors of the host with environmental features and biology and behaviour of the parasite.

1.4 Primate Health and Parasitism

The emergence of infectious disease in primates has become an increasing concern in recent years, in particular after several catastrophic events causing significant impact on wild primate populations. Among the best known examples are recent outbreaks of Ebola haemorrhagic fever in Gabon (Huijbregts et al. 2003; Walsh et al. 2003) and anthrax epidemics (Leendertz 2004) in the Ivory Coast which resulted in the decimation of African ape populations. Understanding, predicting and managing epidemics such as these are important issues for conservation. Nevertheless, the majority of primate pathogens culminate in chronic, sub-lethal infections (Goldberg et al. 2008). However, these infections may be exacerbated by ecological stress and cause significant impairment to biological processes due to immunosuppression, possibly culminating in disease outbreak (Lafferty & Holt 2003).

The primate order is one of the most extensively studied of the mammals, thus offering a wealth of previous knowledge regarding behavioural ecology and evolution. This also allows for potential exploration of pertinent hypotheses in parasitology such as parasites as selective forces on host sociality (Freeland 1976, 1980; Ezenwa 2003). Despite this breadth of opportunity, there have been relatively few studies examining the causal determinants of primate health, likely due to the challenges of obtaining samples from wild primates. The Sabangau PSF provides a particularly suitable study area due to the long-term research conducted and well-habituated animals, thus enabling simple assessment of health via non-invasive sampling methods.

The importance of health monitoring of primate populations and the utilisation of parasitism as an appropriate index is investigated in Chapter 3.

1.5 Parasites and Ecosystems

The ecological role of parasitism on primate survival and conservation is well documented (Wallis & Lee 1999; Cleaveland et al. 2002; Nunn & Altizer 2006; Chapman et al. 2007), however the significance of this assimilation at all stages throughout the ecosystem is often overlooked (Marcogliese 2004; Thomas et al. 2005). Parasites modulate host densities, and particularly for intermediate and final host vertebrate species control the balance between predator and prey species (Seilacher et al. 2007; Magny et al. 2008; Thomas et al. 2009). It has even been argued that healthy ecosystems are those rich in parasites (Hudson et al. 2006).

Understanding ecosystem function necessitates consideration of biodiversity relationships within and across different trophic levels (Duffy et al. 2007). The role of parasitism in ecosystems is inherently related to the dynamics of multiple-species infections and parasite communities (Kuris et al. 2008; Bordes & Morand 2009). It is commonly assumed that although these assemblages play a central, albeit cryptic role in ecological interactions, they contribute only partially to ecosystem biomass. However, observing the universal prevalence of parasites in more detail reveals they make up a substantial quantity of the total biomass of the ecosystem and have even been demonstrated to exceed

predators in representative biomass (Kuris et al. 2008). As parasites make up such a substantial proportion of the environment and exert significant trophic impacts, understanding their place in the ecosystem and predicting how they may affect their host's ecological characteristics is an essential aspect of ecology (Macdonald & Laurenson 2006; Nunn & Altizer 2006).

Recently we have seen a rise in the imperative need to increase our understanding of the value of ecosystem services and the biodiversity that supports these networks of interrelated trophic exchanges (Loreau et al. 2001; Balmford et al. 2002; Duffy et al. 2007). Further to this, recognition is emerging that shifts in biodiversity such as those imposed by biological invasion and rising pathogen quantities as a result of human exploitation of the environment can have a dramatic impact on ecosystem function (Chapin et al. 2000; Sousa 2011). Research contributing to our knowledge of any negative or perhaps positive impacts on biodiversity particularly for more vulnerable endangered species, subsequently has important consequences for conservation.

1.6 The Role of Parasitism in Conservation

The threat posed by parasitism and disease is often viewed as marginal when compared to habitat loss, fragmentation and over-harvesting. However, nutritional and socioecological stress and subsequent disease risks are likely to increase in remaining habitat fragments as human populations expand and further encroach causing greater alterations in landscape ecology and microclimate (Daszak 2001; Chapman et al. 2005a, 2006a; Gillespie et al. 2005b; Hilty et al. 2006; Mbora & McPeek 2009).

The primates of Indonesia are among the most diverse, yet also the most threatened in the world (Nijman 2001; Mittermeier et al. 2009; Gursky-Doyen & Supriatna 2010). Primate population declines are being driven at an unprecedented rate by human activities such as forest conversion and hunting (Cowlishaw 1999; Sodhi et al. 2004; Marshall et al. 2006). Borneo has long been recognised as a biodiversity hotspot with a large species richness of birds, animals and marine life and high rates of endemism (Myers 1988; Myers et al. 2000; Rautner et al. 2005). Reducing levels of biodiversity loss have become priority with many Asian action plans (Eudey 1987; Soemarno 1995; Whittaker 2006) and is critical to conservation measures throughout the region. In order to conserve, it is essential that surveys and biomonitoring programs are conducted in order to assess threat levels to remaining populations and to predict future changes as a result of environmental disturbance as human activities increase in regions of high biodiversity.

Gaining insight into baseline patterns of parasite infections in wild primate populations is of considerable importance with regards to primate conservation as the information can be utilised for the primary stage in understanding dynamics of infectious disease and threats to populations (Cowlishaw & Dunbar 2000; Cleaveland et al. 2002; Whiteman & Parker 2005; Gillespie et al. 2008; Foitová et al. 2009). As described earlier, parasite-host relationships may be influenced by a multitude of different factors (Lewis et al. 2002; Lafferty & Holt 2003; Vitone et al. 2004; Müller 2007). The majority of primate species are affected by encroachment of expanding human populations, adding to the severity and complexity of the issues of primates and infectious disease (Soulsby 1974; Cowlishaw & Dunbar 2000; Woodford et al. 2005; McKenzie 2007; Morand & Krasnov 2010). Anthropogenic disturbance, including habitat destruction from selective logging and forest fragmentation can affect host-parasite interactions in significant ways (Gillespie et al. 2005a, 2005b; Sleeman et al. 2000) and is often associated with an overall greater prevalence of parasite infection (Chapman et al. 2005a, 2006a). As forest is converted to agricultural land or cut down for timber extraction disease risk may be exacerbated by alterations in host susceptibility (Patz et al. 2000; Lafferty & Holt 2003; Ekanayake et al. 2006). Significant fluctuations in biodiversity can have profound effects on ecosystem services that humans rely on, reducing resilience to environmental change and threatening survival of the organisms that are dependent on them (Chapin et al. 2000) illustrated by the primates in the present study. Parasites are an integral element of all ecosystems thus logically nominating them as key indicators of changes in ecosystem health (Marcogliese 2004; Thomas et al. 2009).

It has been proposed that parasites themselves should be included in the IUCN Red List of Threatened Species (Windsor 1990, 1995), not only for their ubiquitous contribution to biodiversity but also in recognition of their utility as bio-indicators, population regulators and bio-engineers (Thomas et al. 2005; Magny et al. 2008; Wilson & Kakouli-Duarte 2009). Whiteman and Parker (2005) highlight that due to the evolutionary rates of parasite DNA, parasites may be unexploited invaluable tools for the management and conservation of endangered vertebrate species; similarly nematodes have long been recognised as potentially extremely useful environmental indicators (Wilson & Kakouli-Duarte 2009).

One fundamental element of epidemiological significance is human health (Wallis & Lee 1999; Cleaveland et al. 2002; Michaud et al. 2003; Doi & Yurlova 2011) and many authors have illustrated the importance of zoonotic transmission between humans and non-human primates (NHPs) (Contacos 1970; Ashford et al. 1990; Leclerc et al. 2004; Rwego et al. 2009; Shakespeare 2009; Krief et al. 2010). The number of pathogens that may be shared between humans and NHPs is still in debate, but values are high at between 61% - 90% (Ashford 2000; Taylor et al. 2001). Indeed it is recognised that a number of major diseases inflicting the world today were of NHP origin, such as HIV-AIDS (Hahn et al. 2000) and several other retroviruses (Wolfe et al. 2004). As a result of human population expansion anthropogenic alterations to the environment may exacerbate the spread of parasites and emerging infectious disease (EID) (Soulsby 1974; Daszak et al. 2001; Woodford et al. 2005; McKenzie 2007; Morand & Krasnov 2010). This further highlights the importance of comparing areas of consistent disturbance with regions of heavier disturbance and gaining baseline patterns of parasite spread in order to understand potential increase in pathogen transmission.

1.7 Project Aims

Through the publication of a series of journal articles, a written report for the local NGO and this MSc dissertation my ultimate aim is to increase the understanding of the dynamics of disease spread and identify threats for primate species in Borneo and elsewhere.

I have divided my specific aims into categories as follows:

1.7.1 Project Aims

1. Gauge health of the primate species living within a tropical PSF using parasitism as a proxy.

- 2. Increase our understanding of understudied primate species and their ecological associations with sympatric primate species.
- 3. Develop a greater understanding of parasite-host relationships and their role in ecosystem function.
- 4. Provide research to foster support for inclusion of parasites in all ecosystem biomonitoring programs.

1.7.2 Project Objectives

- 1. Identify the role of host-intrinsic factors in the parasite infections of primate communities.
- 2. Identify the key threats of the primate communities in PSF and how parasitism affects these ecological relationships.
- 3. Produce a series of articles to appropriate journals.
- 4. Produce a written report for Indonesian research institute and complete MSc thesis.

Chapter Two - Materials and Methods

2.1 Study Site

2.1.1 Indonesian Borneo

Indonesia is home to a rich diversity of primate taxa with over 40 species, half of which are endemic (Gursky-Doyen & Supriatna 2010). A recent report by the IUCN/SSC Primate Specialist Group (IUCN/SCC 2010) revealed that over 70% of Asian primate species and 84% of Indonesian primates are threatened by extinction. Indonesia has been the centre of a broad range of ecological (Davies et al. 1988; Ungar 1995; Yeager 1996; Cheyne 2007) behavioural (Mackinnon 1974; Galdikas 1988; Nekaris 2001; Cheyne et al. 2008), parasitological (Warren et al. 1998; Hasegawa et al. 2003; Jones-Engel et al. 2004; Mul et al. 2007; Foitová et al. 2009; Labes et al. 2010) and conservation-based research (Nekaris et al. 2008; Riley & Priston 2010; Nijman et al. 2011) across a diverse array of primate species.

The island of Borneo is the third largest on the planet and home to 210 mammal species, including 13 primates of which 5 are endemic (Groves 2001). Despite its incredible diversity and large regions of protected areas, Borneo remains the region with one of the highest rates of deforestation in the world. Recent satellite-based surveys reported that Kalimantan lost as much as 56% (>29,000km²) of lowland forest within protected areas between 1985 and 2001 (Curran et al. 2004). Amongst the crises of deforestation for timber and monocultures, fire is one of the most prominent threats to the tropical forests of Borneo and its biodiversity (Mackie 1985; Page et al. 2002; Langner & Siegert 2009).

2.1.2 Sabangau Forest Catchment, Central Kalimantan

The study was conducted in the Sabangau forest catchment in Central Kalimantan, Indonesian Borneo (2° 19' S, 114° 00' E) supported by the organisations CIMTROP (Centre for International Co-operation in Management of Tropical Peat-lands) and OuTrop (Orangutan Tropical Peatland Project) in cooperation with the University of Palangka Raya. The main study area was within a region designated for long-term scientific research known as LAHG (The Natural Laboratory for the Study of Peat-Swamp Forest) which consists of tropical PSF covering over 50,000ha. The Setia Alam field station is situated 20km southwest of Palangka Raya in the upper reaches of the Sabangau River (Figure 2). Well established line transects were available in the 9km² core research area with a transect grid utilised to locate the primate groups. The site has an average rainfall of 2320mm (4-5320mm) and temperature of 26°C (18-36 °C) (Husson et al. 2008).



Figure 2. Detailed map of the study site in the LAHG depicting grid transect and geographic location.

Between 1996 and 1998 the Indonesian authorities developed a massive rice field conversion process that became known as the 'Mega Rice Project' viewed as one the world's worst human-induced environmental disaster (Aldhous 2004). This involved clearing a vast area of the Eastern region of the Sabangau catchment and digging a network of canals to drain the peat. Due to proceeding fires in 1997 and 1998 over 6.5 million ha were affected in Kalimantan, greatly reducing primate and other animal populations, covering the region in smoke and contributing significantly to global greenhouse gas emissions (Page et al. 2002; Aldhous 2004). Between 1973 and 2005 the Sabangau was selectively logged, but remains contiguous forest avoiding major fragmentation effects. Five distinct habitat sub-types varying in structure and vegetation make up the composition of the catchment (Page et al. 1999), which primarily consists of mixed-swamp forest.

Despite the consistent disturbance the Sabangau contains a substantial diversity of flora and fauna, including sixty-four species of mammal (Husson et al. 2007). This forest is of profound importance for the study and conservation of many wild mammal species, in particular for its great diversity of primates. Nine species of primate are known to occur within the reserve, including the largest remaining population of Bornean orangutans (Morrogh-Bernard et al. 2003) and probably the largest population of Bornean agile gibbon estimated at around 30,000 individuals (Buckley et al. 2006; Cheyne et al. 2007) further highlighting the importance for preservation of the Sabangau forest habitat and its inhabitants. The Global Mammal Parasite Database (Nunn & Altizer 2005) and ensuing publications by Hopkins and Nunn (2007) and Gillespie et al. (2008) underscore the lack of primate-parasite data for this region.



Figure 3. Typical transect used to locate the primate species in the Sabangau peat-swamp forest.

2.2 Study Species

The study species involved in this project are the red langur (*Presbytis rubicunda*), classified as Least Concern within CITES Appendix II; and the Bornean orangutan (*Pongo pygmaeus*) and Bornean agile gibbon (*Hylobates albibarbis*) both classified as Endangered within CITES Appendix I (IUCN/SSC 2010; UNEP-WCMC 2011). The Indonesian government has included the Bornean orangutan in the most extensive action plan having developed the Indonesian Orangutan Strategy and Action Plan 2007 - 2017 (Soehartono et al. PHKA 2007). The last official action plan encompassing all Asian primates was that of the IUCN/SSC Action Plan for Asian Primates 1987-1991 (Eudey 1987). Several facets of the primate species selected for this study make them ideal candidates for comparisons of gastro-intestinal parasites, including their high level of habituation and our substantial knowledge regarding overlap in their ecological niches.

2.2.1 Presbytis rubicunda - Red langurs

Red langurs are small arboreal colobines widely distributed across the island of Borneo occurring in almost all protected areas (Supriatna 1986). They live in single-male multi-female units with a polgynous mating system (Supriatna 1986) lacking dominance hierarchies between females of the group (Yeager & KirkPatrick 1998). They are found in primary and secondary forest below 2000m, and although have a preference for primary forest are able to tolerate forests that have been redeveloped after logging has taken place (MacKinnon 1986). Their diet is primarily herbivorous comprising mostly young leaves, seeds and fruits but may resort to a greater degree of gramnivory as seeds become higher in dietary composition in times of lower productivity (Davies et al. 1988). A correlation between group size and home range has been identified with smaller groups having smaller home ranges (Supriatna et al. 1986). They are largely sexually monomorphic, with males being only slightly heavier than females (Fleagle 1999).

To date there is a paucity of literature on red langurs the majority of which is concerned with feeding behaviour (Davies 1984; Supriatna 1986; Davies & Baillie 1988; Davies 1991; Marshall 2009a, b 2010) with limited demographic and ranging information present (Supriatna 1986; Yanuar et al. 1993). No published research examining the parasite communities of wild populations of this monkey species is available and virtually nothing is known about the behavioural ecology of populations living in PSF. Dewitt and colleagues (1991) examined parasite



Figure 4. Adult female red langur (Presbytis rubicunda).

occurrence in three individuals of the *Presbytis* genus, and recovered five gastro-intestinal helminth species common to Asian primates from necropsies of *P. entellus* and *P. senex*. Palmeiri et al. (1977) and Arambulo et al. (1974) also surveyed the parasite infections in Malaysian and Indonesian *Presbytis* spp. but outcomes were restrained by the captive environment.

Although considered Least Concern (IUCN/SSC 2010) the langurs are endemic to Borneo and face threats imposed by anthropogenic disturbance including hunting, disease spread, habitat encroachment and degradation through agricultural expansion and fire resulting in intense rates of habitat loss. The data collected in this study make a valuable contribution to our knowledge of these understudied primates.

2.2.2 Hylobates albibarbis - Bornean agile gibbons

Gibbon taxonomy and phylogeny has remained in dispute for many years with several alterations made to taxonomic distinctions of these small arboreal apes (Creel & Preuschoft 1984; Marshall & Sugardjito 1986; Groves 1989; Brandon-Jones et al. 2004; Geissmann 2007). This is due in part to biogeography, hybridization events, large level of fragmentation

of much gibbon habitat and the difficulty of gibbon field research (Roos & Geissmann 2001; Arnold & Meyer 2006; Marshall et al. 2006; Cheyne 2010). The geographic range of the Hylobatidae family extends across mainland and archipelagic Southeast Asia as far Northwest as India and Bangladesh (Marshall & Sugardjito 1986; Chivers 2001; Chatterjee 2009). The Hylobates genus was formerly divided into four sub-genera (see Groves 1989; Geissmann 1995) which have subsequently been raised to separate genera (Whittaker & Lappan 2009). H. albibarbis was previously classified as a sub-species of H. aqilis and subsequently as Lower Risk, but was recently given species status and listed as Endangered largely due to reduction in large areas of the species' range, including PSF (Geissmann 2007). Planning for conservation measures requires understanding taxonomic differentiation for informing decisions based on population viability and threat status to preserve genetic viability, considering Evolutionary Significant Units (ESUs) as lineages with differentiation in genetics, morphology or ecology (Vogler & DeSalle 1994). This has subsequently encouraged recent developments in genetic and vocalisation techniques to resolve disputes in phylogeography (Roos & Geissmann 2001; Whittaker & Lappan 2009).



Figure 5. Adult male Bornean agile gibbon (Hylobates albibarbis).

Although extra-pair copulations have been exhibited in several studies (Palombit 1992; Reichard 1995), gibbons generally have a monogamous mating system (Raemakers 1979; Fuentes 1998) and live in relatively stable social units including offspring (Bartlett 2007). However, a new perspective of the gibbon's flexibility in socioecology including monogamy and also important insight into gibbons' ecological limitations is now widely acknowledged (Lappan et al. 2009). Gibbons are recognised as playing a central role in forest maintenance and reforestation as they are known to be important seed dispersers (Corlett 1998; McConkey 2009). In areas of high gibbon densities, group ranges often overlap, possibly increasing the chances of encounter rate. This is amplified by their highly territorial nature whereby mated pairs will unrelentingly defend their territory (Cheyne 2010). They share their geographic range with a great diversity of other primates and even other gibbon species (Geissmann 1991). At this study site, gibbons' main encounters were with orangutans (32%) and red langurs (27%) (Cheyne 2010). It has been found that among other sympatric mammal species sharing their forest habitat, orangutans are often the most competitive in terms of resource allocation (Morrogh-Bernard 2003; Cheyne 2010; Marshall 2010).

Limited data are available on *H. albibarbis* (Buckley et al. 2006; Cheyne et al. 2007; Cheyne 2010; Hamard et al. 2010) especially of factors influencing socioecology in PSF. The Sabangau is home to what is likely the largest contiguous population at around 30,000 individuals (Cheyne et al. 2007). Eleven groups and two individual male gibbons have been habituated, with continual follows having been conducted since 2005. Groups have an overlap of 15% with ranges averaging 47ha, and population density an average of 2.6 gibbons/km² (Cheyne 2007).

An assessment in 2003 identified habitat loss, fragmentation and degradation, in addition to hunting and illegal trade as the top threats to gibbon survival (Geissmann 2003). These imminent pressures will inevitably exacerbate the risk of pathogen transmission by mechanisms described earlier (Chapter 1), thus increasing importance of understanding potential for disease risk between these primates, sympatric species and humans in this region. Gibbons have received very little parasitological investigation, the majority of which is concentrated on malarial transmission (Collins et al 1972; DePaoli & Johnson 1978; Leclerc et al. 2004), and little is known of how their unique socioecological characteristics may effect parasite host transmission. This study therefore provides the first insight into these fundamental elements of ecology of gibbons inhabiting PSF.

2.2.3 Pongo pygmaeus - Bornean orangutans

Orangutans are the only extant great ape in Asia. Although at first thought to be one species, the Pongo genus is now separated into two distinct species representing Sumatran (Pongo orangutans abelii) and Bornean orangutans (Pongo pygmaeus) with the latter divided into three separate sub-species (Xu & Arnason 1996; Delgado & van Schaik 2000; Warren et al. 2001; Brandon-Jones et al. 2004). There is now known to be substantial morphological, life history and genetic variation between these taxa (Wich et al. 2009). Orangutans are large-bodied primates with a slow life history (Delgado & van Schaik 2000; Warren et al. 2001; Wich et al. 2004b) and require large contiguous areas of suitable habitat in order to maintain viable populations. They have been shown to be able to survive in



Figure 6. Juvenile Bornean orangutan (*Pongo pygmaeus*).

degraded habitat such as active or former logging concessions, highlighting the importance of incorporating these areas into orangutan management programs (Meijaard 2005; Marshall et al. 2006).

Some of the most comprehensive studies of Bornean orangutans have been conducted in the Sabangau forest catchment, which is home to the largest contiguous population estimated at around 6,900 individuals (Marshall et al. 2009; Morrogh-Bernard et al. 2003). The mixed-peat forest region where I conducted this research supports the majority of the total orangutan population in the Sabangau (Morrogh-Bernard et al. 2003) although densities are relatively low compared to other regions (Husson et al. 2008). Sociality of orangutans has been the subject of a large amount of field studies (e.g Mackinnon 1974; Mitani 1985; Galdikas 1985; van Schaik 1999; Mitra-Setia et al. 2008). Support is growing for a shift from viewing orangutans as solitary to having a complex social organisation which varies between the species with loose communities structured around a dominant flanged male (see Mitra-Setia et al. 2008). The Sabangau PSF has regular fruit availability which has subsequent consequences for orangutan density and feeding strategy, thus possibly influencing parasite transmission and potential disease spread. This will be discussed in more detail in Chapter 4.

Unlike the other two study species, orangutans have been the subject of several studies focussing on health indices (Warren et al. 1998; Kilbourn et al. 2003; Schmidt et al. 2006; Mul et al. 2007; Labes et al. 2010), and we have gained substantial knowledge on the gastrointestinal parasites of both captive and free-ranging orangutans (Collet et al. 1986; Foitová 2002; Kilbourn et al. 2003; Foitová et al. 2009; Labes et al 2010; Hegglin et al. 2010). I may therefore predict a general continuity of parasite community as a baseline, and logically apply this to the sympatric species as an expectation of transmission of generalist parasite species between multiple hosts. Inter-specific competition can have profound effects on the availability of food resources distributed in primates' ranges (Pianka 1974; Tutin et al. 1991) and has implications for transmission of parasites across multiple host species (Huffman & Chapman 2009). Therefore, when recognising the potential of other suitable hosts acting as reservoirs and habitat patches for parasites, niche differentiation and overlap may be fundamental drivers for maintaining parasite transmission between species. As orangutans are known to have large overlap in ecological niche with both gibbons and langurs (Morrogh-Bernard et al. 2003; Marshall 2009; Cheyne 2010), they act as suitable candidates for elucidating key determinants in socioecological characteristics that may affect parasite transmission and emergence of infectious disease.

2.3 Faecal Sampling Methods

2.3.1 Faecal Sample Collection

Non-invasive data collection occurred from all age-sex categories of three habituated primate species: Bornean orangutan, Bornean agile gibbon and Bornean red langur over a period of 14 weeks (April – July 2011). Faecal samples were obtained opportunistically whenever defecation was observed and stool located, and stored in Universal 30ml vials with at least 2 grams of faecal matter. GPS points were taken and the date and time of collection, age-sex category and name of individual, study group and consistency of the faeces were labelled. Before processing samples were examined macroscopically for the presence of larval or adult helminths, blood and mucus. Samples were stored in 10% formalin until available for processing at the University of Palangka Raya (UNPAR) laboratory.

2.3.2 Sample Processing

Samples were processed as soon as possible after defecation. Faecal floatation and sedimentation techniques with sodium-nitrate solution were utilised in order to separate gastro-intestinal helminth ova and larval stage helminths and protozoa from the faecal matter (Gillespie 2006). Using gloved hands approximately 1g of faeces was placed into a 15ml centrifuge tube using a wooden applicator stick. The tube was filled $^2/_3$ of the way with de-ionised water and homogenized with a wooden spatula, then centrifuged for 10 minutes at 1800 rpm. The supernatant was decanted and the faeces re-suspended in NaNO₃ solution. The tube was filled to the meniscus with NaNO₃ and a cover slip placed on the lip of the tube then left to sit for 10 minutes. The cover slip was removed and placed on a labelled slide.

Faecal smears utilising iodine aided in identification of protozoa. Single slides for each individual sample were systematically scanned using a compound light microscope under 10X and 40X magnifications. Presence of parasitic helminths and protozoa were reported, and photographs taken of every unique individual parasite found within each slide. Aided by

an ocular micrometer morphology, size, shape, colour and overall appearance of ova and larval helminths and trophozoites and cystic protozoa were recorded in order to accurately identify parasitic taxa. Photographs, identification keys and charts from available literature assisted in this (Zaman 1984; Ash et al. 1994; WHO 2004; Huffman & Chapman 2009). Images were sent to London School of Tropical Medicine in order to identify unknown and confirm proposed parasite taxa.

2.3.3 Assessment of Parasite Community

Parasite infections were described with terms standardised by Bush et al. (1997) as prevalence of individual parasites, species richness, multiple-taxa-infections and parasitic output (eggs/g) with respect to each individual sample and for each primate collectively. Although prevalence is the most commonly reported and least mis-used of ecological terms in parasitology (Bush et al. 1997) due to a number of confounding factors it does not accurately represent a measure of infection intensity (Gillespie 2006). However, it is a sufficient indicator of infection status of an individual and cumulatively of the study population (Gillespie 2006).

Samples were tested on an individual basis rather than pooling all samples. Normality of data was assessed by use of the Kolmogorov-Smirnov test. Chi-square (X^2) tests for non-parametric data were utilised in SPSS v.17 to test for variation between the study groups with significance using p value <0.05. In order to normalise data, all data were log transformed (x - 1) for each parasite taxa and total output before performing statistical tests. Analyses of variance (one-way ANOVA) were performed to make cross-comparisons of parasitic output means between the primate species. Spearman's rank correlation coefficient (R_s) was applied to identify inter-specific associations between socioecological variables and indices of parasitism (Table 3). Although R_s is an extremely useful measure of the substantive importance of an effect, it cannot be used to unequivocally identify causal relationships. I utilised this test to provide a logical connection between variables however more detailed analyses from long-term parasite surveillance utilising a larger sample size will be valuable to understand these relationships in greater depth.

2.3.4 Additional Dissertation Details

I have researched this topic thoroughly in order to gain a broad perspective from multiple sources and have created not only a comprehensive synthesis of previous findings but also my view on well-supported arguments. I have confidence my data and arguments are suitable for the proposed journals. I have subsequently formatted chapters 3 and 4 to appear as they would in publication format for preparation time-saving, aesthetics and ease of reading.
Chapter Three - Article One

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COMMENTARY

Creating Connections: Integrating Health Monitoring Into Primate Conservation Management

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ABSTRACT

Despite the prominence of maintaining viable populations of wildlife and ensuring human health, there has been a lack of attention paid or practical input given into disease management procedures in many conservation biology projects. We argue that efficient techniques such as parasite surveillance should be integrated into systematic monitoring programs to develop our knowledge of disease transmission, reduce potential outbreaks and augment the health of biodiversity throughout the ecosystem. *Key words*: Biomonitoring; Conservation-Medicine; Disease; One-Health; Parasite; Pathogen

CONSERVATIONISTS FACE MANY CHALLENGES IN MAINTAINING PROTECTION OF SPECIES AND THEIR HABITAT, often as a result of inadequate enforcement of protected areas and diminishing financial stability. However, one of the most serious yet underappreciated threats to biodiversity is frequently left on the backburner. Disease outbreak can pose a serious challenge to conservation efforts, particularly in the development of wildlife re-introduction programs (Woodford 1993; Cunningham 1996), ecotourism (Muehlenbein & Ancrenaz 2009) and preservation of small fragmented populations (Marsh 2003). The past three decades have seen remarkable developments in our knowledge of primate behaviour, ecology and evolution. Yet despite the importance of health for the survival of these species, fundamental gaps remain in our understanding of how socio-ecology and behaviour affect the dynamics of infectious disease. With this commentary we present an overview of health throughout ecosystems using the appropriate case of non-human primates. We emphasise the recognition of parasites as integral elements of ecosystem function, and in particular point to the value of simple, cost-effective and non-invasive sampling techniques in order to assess community assemblages and inter-specific pathogen transmission.

Issues of mis-communication and detachment at the interface between the environment, wildlife, humans and domestic animals are all-too-often neglected, much to the on-going detriment to security of protected areas. We encourage the unity of these elements and implementation of the 'One Health Perspective', a paradigm for effective broad-scale management of disease, which Osofsky and colleagues (2005, p.67) describe as "not about interfering with nature - it is about trying to help systems already perturbed by pathogens that may or may not "belong" within them to re-establish a state wherein disease does not threaten vital conservation and development objectives." Inadequate expertise or funding deficits often restrict potential of progress evaluation and health monitoring. A natural trade-off between other land-use practices, regions of expansion and agricultural developments inevitably occurs if investing resources in health programs, thus stimulating the requirement for cooperation between epidemiologists, development specialists and protected area managers to maximise efficiency of resource-use. By encompassing all components of biodiversity that are under threat in a wellorganised manner with systematic evaluation and feedback, a more effective system of management may be established.

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One fundamental issue that we face is the division between conservation biologists and field practitioners, whereby disconnection between the dissemination of information and practical implementation of knowledge may be a central caveat to augmenting the potential of information derived from primate health assessment. Interdisciplinary approaches with dialogue between all stakeholders are essential to ensure long-term protection of vital habitats and biodiversity.

Primates represent ideal candidates for the investigation of ecosystem health due to three pertinent attributes: (1) The majority of primates are diurnal, relatively large-bodied and throughout the mammals have been thoroughly studied in terms of behavioural ecology and evolution. (2) Primates are generally gregarious, highly social mammals thus having major implications for the spread of pathogens between individuals of a population. (3) Their close phylogenetic similarity to humans leaves us susceptible to many of the same generalist parasites and diseases. Primates have been shown to augment conservation efforts as representative flagship species, facilitating support of projects aimed at protecting their habitat and its biodiversity (Mittermeier 1988; Dietz et al. 1994). Additionally, primates are efficient seed-dispersers and often represent a key element in maintenance and regeneration of forest habitat (Corlett 1998; McConkey 2009) thus sustaining the network of health throughout the ecosystem.

FOUNDATIONS OF HEALTH

The health of an individual may be determined by its state of homeostasis, the dynamic system of internal physiological processes. A healthy host retains a balance of micro-organism communities of bacterial, helminthic and protozoan species (Roberts & Janovy 2008). However, dynamics can alter with fluctuations in stress levels, in addition to individual host traits such as age, sex, diet and the presence of exogenous microorganisms including other parasite species (Ryan et al. 2010) with the potential to overwhelm the host resulting in outbreaks of disease. Parasitology not only enables us to gain valuable information about the diversity of parasites infecting populations, it also provides insight into the general condition of the host. Once we recognize that most living organisms are parasitic and that parasites are integral to ecosystem processes we see the inherent need to further our understanding of their impacts on the species we aim to protect.

Disease ecology has largely been ignored in the past by conservation biologists with outbreaks treated as random catastrophic events (Lyles & Dobson 1993). Empirical evidence has reiterated the importance of monitoring health with major population declines attributed to outbreaks of disease (e.g Walsh et al. 2003). However, this field of investigation has started to gain ground recently and major new developments in biomonitoring programs have implemented disease ecology into their remit. The emergence of conservation medicine holds potential for the successful marriage of our knowledge of pathogens and physiology with our understanding of ecological processes and society. In order to conserve in the maelstrom of human activity in regions of high biodiversity, it is essential that epidemiological surveys and biomonitoring programs are conducted to assess threat levels of remaining populations and to predict future changes as a result of environmental disturbance.

PRIMATES AND DISEASE

Emerging infectious disease may be described as 'diseases that have recently increased in incidence or geographic range, recently moved into new host populations, recently been discovered or are caused by newly-evolved pathogens' (Daszak et al. 2001). Given the ubiquitous nature of parasites, they may act as useful indicators for the health of individuals and provide valuable insight into the condition of the population and the threats that it faces. Viruses are the principal cause of most disease-associated primate population crashes (e.g. Huijbregts et al. 2003; Walsh et al. 2003) and gastrointestinal parasite infections are usually characterised by chronic, sub-lethal infections. However, if hosts become significantly ecologically stressed, the infection may culminate in adverse health impacts from immunosuppression. This in turn affects population demographics (especially after an epidemic) and subsequently influences predator avoidance, within group resource and mate competition and inter-specific competition between sympatric species (see Nunn & Altizer 2006; Huffman & Chapman 2009) even resulting in mortality and population declines (e.g Dunbar 1980; Palombit 1992).

There are a wide-range of tools and techniques available to veterinarians, ecologists and conservation biologists that can provide an index of primate health. Non-invasive sampling is often valued for its relatively low impact on the study species, with parasitological information readily available via examination of faecal samples collected from individuals of the population. However, a look through the literature reveals a variety of different approaches. From a comprehensive assessment covering a wide-range of parasite taxa we recommend faecal floatation and sedimentation techniques utilising sodium-nitrate solution, as described and suggested by Gillespie (2006). With greater standardization of survey methods, the value of our interpretations and potential for comparative studies and meta-analyses increase exponentially.

INDICATORS AND MONITORING FOR ECOSYSTEM HEALTH

Our study site in the Sabangau peat-swamp forest catchment in Central Kalimantan, Indonesian Borneo contains nine primate species, of which extensive research has been conducted on Bornean orangutans (Pongo pygmaeus), Bornean agile gibbons (Hylobates albibarbis) and recently incorporating the little-studied red langurs (Presbytis rubicunda) with establishment of a broad-scale ecological survey effort. This is an incredibly important conservation site with long-term study of tropical peatlands, whilst containing the world's largest populations of orangutans at as many as 8,900 individuals (Morrogh-Bernard et al. 2003) and probably the largest population of Bornean agile gibbons estimated at around 30,000 individuals (Buckley et al. 2006; Cheyne et al. 2007). We argue the critical value of maintaining support for ecological monitoring programs, especially long-term research efforts (Husson et al. 2007). By recognising a system of key indicators such as energy balance, population size and parasite levels of keystone species to monitor biodiversity and ecosystem health over time, integrity of the habitat can be maintained throughout all levels. In recognition of this fundamental facet of health monitoring for conservation efforts, our current research into distribution, population status and behavioural ecology of these primates incorporates several health indices. These include ketone analyses, dietary assessment related to fluctuations in spatial and temporal food availability and parasitological surveys examining potential pathogen trends between the primate species (see Chapter 4).

Critics of primate research caution the rational possibility of introducing novel pathogens to study populations, as has been the case with some ecotourism ventures. After almost two decades of researching primates in the Sabangau, we have found no evidence of anthroponotic disease spread. Epidemiological monitoring, encompassing human parasite surveys around the site will enable us to keep track of this, supplementing adherence to field protocols to minimise transmission potential. Focus on monitoring health indicators is high in our agenda, as fluctuations over extended periods may be significant determinants of the ecosystem being compromised.

Researchers collaborating with local NGO CIMTROP (Centre for International Co-operation in Management of Tropical Peat-lands) have been studying the distinctive peat-swamp forests since 1993, revealing startling findings about the hydrology and carbon storage function of tropical peat-lands. Partnerships between the University of Palangka Raya, CIMTROP and OuTrop (Orangutan Tropical Peatland Project) have enabled a multi-faceted approach to biodiversity monitoring, encompassing different elements throughout the ecosystem, with implications for the health and well-being of local people as well as preservation of vital habitat for primate species and other wildlife. Long-term sites such as these are valuable as models for other locations in tropical rainforest habitat, and only by combining disciplines and cooperating will we be able to determine by which mechanisms disease poses an obstacle to conservation efforts.

We have collated a series of examples of primate health assessments from sites that have incorporated parasite surveillance into their remit across a range of primate species. The details of these and key findings of their research are presented in Table 1. This exemplifies how we can disseminate findings between sites and build on these to enable active conservation measures to be undertaken.

TABLE 1. Key findings of previous health assessments of primates utilising faecal sampling methods as an index of health.						
Primate species	Location	Key findings of research	Source			
Toque macaque; grey langur, purple-faced langur	Polonnaruwa, Sri Lanka	Cryptosporidium found in high levels all three species; 96% co-infected with other parasite species; indication of direct public health risk due to high potential zoonotic transmission of pathogenic protozoa.	Ekanayake <i>et al.</i> 2009			
Tana river red colobus	Western Uganda	Parasitism & poor nutrition lead to stress of endangered primates: Faecal-cortisol levels increased with lower food availability; cortisol levels correlated with increase in parasite infections.	Chapman <i>et al.</i> 2007			
Western chimpanzee; Guinea baboon	Fongoli, Senegal	Low prevalence of pathogenic parasites & high prevalence of symbiotic protozoa in chimpanzees indicate good health; high prevalence of pathogenic parasites in baboons indicates transmission potential to threatened population.	Howells <i>et</i> <i>al.</i> 2011			
Black howler monkeys	Belize and Mexico	Anthroponotic pathogen transfer suggested from presence of Giardia infections in howler monkeys; indication of importance of cross-species transmission between other primate species.	Vitazkova & Wade 2006			
Western lowland gorilla	Central African Republic	Relatively low parasite prevalence found indicates good health; baselines provided as part of comprehensive health-monitoring program investigating impacts of ecotourism.	Freeman <i>et</i> <i>al.</i> 2004			
Six macaques endemic to Sulawesi	Peninsular Sulawesi, Indonesia	Assessment of 88 pet primates revealed high susceptibility of shared generalist parasites; relatively low proportion pathogenic although some potential for zoonotic/anthroponotic transmission identified – human pathogens probable threat to endangered primate species.	Jones-Engel <i>et al.</i> 2004			
Red langur; Bornean orangutan; Bornean agile gibbon	Central Kalimantan, Indonesian Borneo	First parasite assessment of wild red langurs and gibbons – baseline data of parasite communities established; host density positively associated with high parasite levels; relationship between inter-specific competition and density with highest parasite burdens in langurs.	Hilser <i>et al.</i> 2011			

SYNTHESIS

Careful consideration of the spatial arrangement and connectivity of primate populations, coupled with proactive management of health measures should reduce the risks of development and spread of infectious disease. The inclusion of health monitoring programs, such as those implemented in several field sites identified as important to the survival of primate populations, and the unification of conservation biologists and health practitioners is crucial with escalating risks of disease between primate species. It is the connection between the small and cryptic with the great and charismatic, illustrated aptly by the ubiquitous presence of parasites and the diminishing primates that remind us of the complexity of biodiversity, spurring us to broaden our perspectives and adopt multi-disciplinary approaches.

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Chapter Four - Article Two.

RESEARCH ARTICLE

Socioecology and Gastro-Intestinal Parasites of Sympatric Primate Species Inhabiting the Sabangau Peat-Swamp Forest, Central Kalimantan

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The parasite communities of sympatric primate species red langurs (*Presbytis rubicunda*), Bornean orangutans (*Pongo pygmaeus*) and Bornean agile gibbons (*Hylobates albibarbis*) were examined in order to monitor changes in susceptibility and the dynamics of emerging infectious disease. Sodium-nitrate floatation and sedimentation methods were utilised to recover gastro-intestinal parasites of the three primate species. Parasitism was measured in terms of prevalence, parasitic output, richness and multiple species infections. Within all primate species a rich diversity of parasite taxa were identified, with langurs generally harbouring greater infections, whilst orangutans had more substantial helminth infections. Protozoa recovered included *Entamoeba coli, Entamoeba histolytica/dispar, Balantidium coli* and *Blastocystis hominis*. Helminths included *Trichuris trichuria, Strongyloides* sp., *Enterobius vermicularis, Ascaris lumbricoides, Trichostrongylus* sp., *Schistosoma mansoni* and a species of hookworm. Whilst providing a baseline for parasite communities of wild gibbons and red langurs, we find a large overlap in the community assemblage of parasite species, with langurs harbouring greatest parasite prevalence and species richness. Relationships between environmental, behavioural and ecological factors were identified as causal determinants of parasite community diversity, calling for greater incorporation of parasitic research into conservation and monitoring programs to maximise information obtained from ecosystem-based studies. © 2011 Wiley-Liss, Inc.

Key words: conservation; disease; ecology; gibbon; langur; orangutan; pathogen

INTRODUCTION

Borneo is home to thirteen primate species, five of which are endemic [Groves, 2001]. The Sabangau forest catchment in central Kalimantan has recently been recognised as one of the most important regions for conservation of these primate species and is home to the largest population of Bornean orangutans (*Pongo pygmaeus*) [Morrogh-Bernard et al., 2003] and what is likely the largest population of Bornean agile gibbons (*Hylobates albibarbis*) [Buckley et al., 2006; Cheyne et al., 2007]. Although data are currently lacking for red langurs (*Presbytis rubicunda*), this region is also likely to be of high importance for this endemic primate species with an ecological survey currently being conducted to assess threat status.

The interactions that occur between parasites and their hosts are numerous and multifaceted [Bush, 2001;

Lafferty and Holt, 2003; Vitone et al., 2004]. These parasite-host relationships have been thoroughly investigated for single host/parasite species. However, hosts are typically parasitized with multiple parasite taxa which are shared between sympatric species within the region, highlighting the importance of understanding the cumulative effects of poly-parasitism [Bordes and Morand, 2009; Poulin, 1997].



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With such a diversity of mammals including primates living within this unique habitat type, the possibility of cross-transmission between different species is a considerable factor that should be taken into account for disease spread [Ezenwa, 2003; Dewitt et al., 1991; Müller 2007]. This is also exemplified by substantial evidence demonstrating a rise in parasite levels in hosts exposed to anthropogenic disturbance and greater exposure to a greater diversity and more novel pathogens [Chapman et al., 2005; Daszak et al., 2001; Ekanayake et al., 2006; Weyher et al., 2006]. The connection between primate socioecology and disease risk remains largely untested. Freeland [1976] developed a series of hypotheses to explain some of the dynamics of these interacting factors. However, in comparison to other aspects of ecology such as predation, disease dynamics have been relatively understudied.

Ecological dynamics such as fecundity, survival and reproduction rely on maintaining health of a population. Therefore, disease may be a key determinant of population growth and viability [Anderson and May, 1978]. A healthy host retains a balance of micro-organism communities of bacterial and protozoan species [Roberts and Janovy, 2008]. However, proportions can vary with fluctuations in stress levels, in addition to individual host traits such as age, sex, diet and the presence of exogenous microorganisms including other parasite species [Ryan and Ray, 2010] with the potential to overwhelm the host causing outbreaks of disease.

Viruses are the principal cause of most diseaseassociated primate population crashes [Huijbregts et al., 2003; Walsh et al., 2003] and gastro-intestinal parasite infections are usually characterised by chronic, sub-lethal infections [Goldberg et al., 2008]. However, if hosts become significantly ecologically stressed, the infection may culminate in adverse health impacts from immunosuppression. This in turn affects demographics, predator avoidance, within group resource and mate competition, and inter-specific competition between sympatric species [Altizer et al., 2003; Daszak et al., 2000; Huffman and Chapman, 2009; Nunn and Altizer, 2006] even resulting in mortality and population declines [e.g Dunbar, 1980; Palombit, 1992].

Monitoring these processes is valuable for conservation management as the information can indicate ecological stress and the impacts of disturbance [Chapman et al., 2007; Cleaveland et al., 2002; Stuart and Strier, 1995]. Primates are subjected to a wide range of socioecological factors that influence the potential for parasite establishment and spread [Hausfater and Meade, 1982; Huffman and Chapman, 2009; Lafferty and Holt, 2003]. These factors may be directly related to the individual host, the group or population of potential hosts, the environment in which parasites may be spread and the biology and transmission strategies of the particular parasites themselves [Lewis et al., 2002; Roberts and Janovy, 2008]. Larger groups in denser populations will likely have greater parasites spread directly through social contact [Freeland, 1976; McGrew, 1989]. Studying the interactions between competing species and highlighting how socioecological factors interact to affect gastrointestinal parasite transmission has implications for understanding the spread of all pathogens and can provide insight into disease transmission.

An investigation into congeneric differentiation in niche exploitation was conducted to elucidate the associations between primate species and their parasite burdens. Socioecological variables most likely to play a central role in determining parasites were assessed in all three primate species for any correlation with indices of parasite infection including total protozoan infection, total helminth infection, parasite species richness (PSR) and total prevalence. With this parasitological assessment in a uniformly disturbed peat-swamp forest baseline data are provided for future epidemiological research and insights into parasite spread in sympatric primate species.

METHODS

Study Site [see section 2.1]

Study Species

[see section 2.2]

Experimental Design

[see section 2.3]

The research complied with protocols approved by the American Society of Primatologists with ethical guidelines for the treatment of non-human primates, was approved by the appropriate animal care and use committees (i.e. Oxford Brookes University, UK) and followed Indonesia's laws for foreign research.



Fig. 7. Log transformed (x - 1) parasitic output (ova/larvae/cysts/trophozoites per gram) for orangutans, gibbons and langurs and in the Sabangau peat-swamp forest, Indonesian Borneo.

RESULTS

Parasite Taxa Recovered

One-hundred and twenty two faecal samples were collected from five groups of langurs, four groups of gibbons and nine individual orangutans. A total of fourteen taxa of parasites were recovered, including six species of nematode, a trematode and five species of Nematodes recovered included Ascaris protozoa. lumbricoides, Enterobius vermicularis, Strongyloides sp., Trichostrongylus sp., Trichuris trichuria, hookworm sp. and unidentified helminth. A digenetic trematode an Schistosoma mansoni was also found in the gibbons and langurs but was absent from the orangutans. Infections of included Entamoeba coli, protozoa Entamoeba histolytica/dispar, Balantidium coli, Blastocystis hominis and an unidentified protozoan. Langurs were parasitised by thirteen different parasite taxa, whilst gibbons harboured twelve and orangutans eleven (Table II).

A potential symbiont involved in cellulose digestion and a possible indicator of health (see discussion), *Troglodytella abrassarti* was recovered in half of orangutans and 10% of gibbons surveyed but was absent from the langurs ($\chi^2 = 11.656$, df = 1, P = <0.001).

Parasitic Output

Once data were log transformed (x - 1) for normalisation, a significant difference in overall parasitic output between the primate species was found (F = 5.894; df = 2; P = 0.004) (Figure 7). Orangutans had the highest overall output of helminths (F = 3.320; df = 2; P = 0.040) whilst langurs had a substantially higher protozoa output (F = 22.004; df = 2; P = <0.001). Within the parasite taxa the output was similar between the primate species (P = >0.05), apart from elevated output of *Entamoeba coli* in langurs (F = 5.423; df = 2; P = 0.08) and hookworm in orangutans (F = 4.068; df = 2; P = 0.024). Langurs also had the highest number of unique parasite taxa in each sample (PSR) (F = 3.287; df = 2; P = 0.041).

Parasite Prevalence

Table II depicts the prevalence values and variation between the orangutans, gibbons and langurs. Orangutans had greatest prevalence values for a number of helminth taxa including *Enterobius vermicularis*, *Trichostrongylus* sp. and hookworm sp. Langurs had the highest prevalence of *Trichuris trichuria* and also the highest protozoa prevalence overall and for three individual protozoa taxa. Gibbons had the lowest prevalence values in all associations.

Devecite Texe	% Prevalence					
Parasite Taxa	Orangutan	Gibbon	Langur	χ²	df	Р
Nematodes						
Ascaris lumbricoides	16%	30%	17%	2.7	2	0.259
Enterobius vermicularis	25%	7%	8%	6.545	2	0.038*
Strongyloides sp.	19%	13%	13%	0.551	2	0.759
Trichostrongylus sp.	44%	10%	5%	24.05	2	<0.001***
Trichuris trichuria	6%	0%	28%	15.079	2	<0.001***
Hookworm sp.	56%	47%	28%	7.468	2	0.024*
Unidentified helminth	22%	23%	22%	0.034	2	0.983
Trematodes						
Schistosoma mansoni	0%	10%	10%	3.455	2	0.178
Protozoa						
Entamoeba coli	22%	40%	57%	10.473	2	0.005*
Entamoeba histolytica/dispar	9%	23%	52%	18.611	2	<0.001***
Balantidium coli	0%	17%	47%	25.206	2	<0.001***
Blastocystis hominis	0%	0%	12%	7.674	2	0.220
Troglodytella abrassarti	50%	10%	0%	40.621	2	<0.001***
Unidentified protozoan	13%	17%	3%	4.976	2	0.083
Total helminth infection	81%	60%	62%	4.316	2	0.116
Total protozoan infection	41%	53%	82%	17.184	2	<0.001***
Protozoan & helminth infection	28%	27%	45%	29.320	8	<0.001***
Total Parasitised	94%	87%	97%	2.113	2	0.348

TABLE II. Prevalence and Representative Associations of Total Parasite Community Recovered from Orangutans,Gibbons and Langurs in the Sabangau Peat-Swamp Forest, Indonesian Borneo.

Significant results in bold, reported with P value < 0.05 = *, P value < 0.005 = **, P value < 0.001 = ***

We tested for the potentially confounding factor of sex and found no variation between the total helminth infections ($\chi^2 = 0.871$, df = 1, P = 0.243), total protozoan infections ($\chi^2 = 3.302$, df = 1, P = 0.055) or total prevalence of infection of any parasite type ($\chi^2 = 0.369$, df = 1, P = 0.429). However, total Infections of the protozoa *Entamoeba histolytica/dispar* were found in greater numbers in females than in males ($\chi^2 = 6.126$, df = 1, P = 0.013). Within the sample of orangutan males, we also tested for dominance by comparing parasite burdens of flanged and unflanged individuals, but found no significant differences between individual parasite taxa or total parasitic infection (χ^2 = 0.768, df = 2, P = 0.681).

Across all three primate species, age played an insignificant role in determining parasitic output (F = 1.147; df = 1; P = 0.287) and PSR (F = 1.147; df = 1; P = 0.287) although adults harboured greater loads of *Ascaris lumbricoides* (F = 19.122; df = 1; P = <0.001).

There were no correlations between the socioecological variables tested and the total overall prevalence (Table III). Increases in body weight and home range were positively associated to the same degree with a rise in the number of individuals infected with at least one helminth parasite ($r_s = 0.163$; N = 122; P = 0.036).

	Socioecological Variable							
Parasitism	Body	Group	Density	Home	% Diet	% Diet	% Diet	% Diet
Index	weight	size		range	leaves	fruit	flowers	inverts
Total helminth	0.163*	-0.147	-0.147	0.163*	-0.147	0.147	-0.98	0.147
prevalence								
Total protozoa	-0.105	0.374**	0.374**	-0.105	0.374**	-0.374**	0.363**	-0.374**
prevalence								
Both infections	-0.18	0.932**	0.932**	-0.18	0.932**	-0.932**	0.996**	-0.932**
PSR	0.005	0.197*	0.197*	0.005	0.197*	-0.197*	0.023**	-0.197*
Total	0.098	0.086	0.086	0.098	0.086	-0.086	0.128	-0.086
prevalence								

TABLE III. Correlational Matrix of Socioecological Variables for Primate Community with Five Indices of Parasite Infection.

Significant results in bold, reported with P value < 0.05 = *, P value < 0.005 = **, P value < 0.001 = *** Am. J. Primatol. DOI 10.1002/ajp Larger groups were shown to be associated with having a greater overall prevalence of infections with protozoa and was highly positively associated with individuals showing co-infection with both protozoa and helminths ($r_s = 0.374$; N = 122; <P = 0.001). Following this trend, as the percentage of leaves and flowers in the diet increased so did the protozoan infections, whereas a diet containing more fruit and invertebrates was associated with lower protozoan infections (Table III).

Interestingly, although no association between total helminth prevalence and dietary composition was found, positive correlations were found between percentage of invertebrates in the diet and greater infections of *Enterobius vermicularis* ($r_s = 0.179$; N = 122; P = 0.024), *Trichostrongylus* sp. ($r_s = 0.395$; N = 122; <P = 0.001), and hookworm ($r_s = 0.247$; N = 122; P = 0.003), although other factors contributed highly to the outcomes of these interactions. Parasite diversity in each sample (PSR) was positively associated with group size ($r_s = 0.197$; N = 122; P = 0.015), density ($r_s = 0.197$; N = 122; P = 0.015) and the percentage of leaves ($r_s = 0.197$; N = 122; P = 0.015) and flowers ($r_s = 0.213$; N = 122; P = 0.015) in the diet. Most of

the variation in parasite prevalence and richness reported was explained by population density.

DISCUSSION

An investigation into congeneric differentiation in socioecological variables revealed associations between parasitic communities of three sympatric primate species in a peat-swamp forest. Using several indices of parasitism langurs were consistently found to have the highest levels of parasitism in this study population, whilst gibbons had significantly lower infections across all parasite taxa. Despite variations in specific parasite taxa, a large proportion of parasites found (N= 10) occurred in all three primates, indicating a substantial amount of parasite transmission between sympatric primates at this site. Literature is sparse for parasite assessments in langurs and gibbons. From the Presbytis genus, records of the presence of Strongyloides sp., Trichuris trichuria and Enterobius vermicularis. have been reported [Arambulo et al., 1974; Dewitt et al., 1991; Palmeiri et al., 1977] which occurred at relatively high levels in this study.

TABLE IV. Socioecological Characteristics Likely to Affect Parasite Prevalence and Species Richness of Orangutans, Gibbons and Langurs in the Sabangau Peat-Swamp Forest, Indonesian Borneo.

Socioecological					
Variable	Orangutan	Gibbon	Langur		
Body size (mean)/kg	M: 78kg F: 37kg ^{1.}	M: 6.4 kg F: 5.5 kg ^{2.}	M: 6.2kg F: 5.7kg ^{3.}		
Group size (mean no.					
individuals)	1.1 4.	5 ^{4.}	7.5 ^{4.}		
Density					
(individual/km ²)	2.4 km ^{2 5.}	2.6 km ^{2 6.}	16.5 km ^{2 7.}		
Home range (ha)	406 ha ^{8.}	47 ha ^{6.}	67 ha ^{9.}		
Diet					
% folivory	5% ^{10.}	25% ^{6.}	36% ^{9.}		
% frugivory	74% ^{10.}	63% ^{6.}	52% ^{9.}		
% flowers	5% ^{10.}	5% ^{6.}	12% ^{9.}		
% invertebrates	9% ^{10.}	1% ^{6.}	<1% ^{9.}		
Social & mating system	Polygamous; semi-solitary – hierarchy organised around flanged male ^{10.}	Monogamous; pair- bonded; family groups ^{6.}	Polgynous; single-male multi-female ^{9.}		
Strata use	Moderate terrestrial behaviour observed ^{8.}	11-15m preferential; wholly arboreal ^{6.}	Predominantly arboreal; terrestrial behaviour observed ^{11.}		

Sources: 1. Jungers [1985]. 2. Payne et al. [1985]. 3. Oates et al. [1994]. 4. This study – average from all groups sampled.
 5. Morrogh-Bernard et al. [2003]. 6. Cheyne [2010]. 7. Nijman [25 study average - *pers. comm.*]. 8. Morrogh-Bernard [2009]. 9. Supriatna [1986]. 10. Morrogh-Bernard et al. [2008]. 11. Davies [1984]; Davies et al. [1988].

Previous research examining gastro-intestinal parasites of colobines [Chapman et al., 2005a; Ekanayake et al., 2006; Gillespie et al., 2005a] and orangutans [Collet et al., 1986; Labes et al., 2010; Mul et al., 2007; Warren, 2001] indicates continuity with earlier findings covering all parasite taxa recorded in this study. The parasitic communities described here for wild red langurs and gibbons provide a baseline for these species as to the best of our knowledge this is the first published survey examining their gastro-intestinal parasites. It can be observed from our data that overall all three species have relatively high levels of parasitic prevalence and species richness, but relatively low parasitic output, with samples commonly yielding only a few individual eggs, larvae, cysts trophozoites. When compared across species or orangutans had the greatest output of hookworm and total helminth output. They also had significantly higher prevalence of Enterobius vermicularis, Trichostrongylus sp. and hookworms than the other two species. Aside from this reported high burden of gastro-intestinal helminths, orangutans had far lower levels of protozoa than langurs and gibbons, with both Blastocystis hominis and the pathogenic Balantidium coli being absent in orangutan samples. Mul et al. [2007] also reported a relatively low protozoan level in the gastrointestinal parasite communities of free-ranging Sumatran orangutans.

The low presence of protozoa in the orangutans of this study may be an indicator of good health for this population. Balantidium coli, the only pathogenic ciliate known to infect humans [Schuster and Ramirez-Avila, 2008] was found in relatively low prevalence in gibbons and langurs but absent from orangutans. Strongyloides sp., the most commonly occurring helminth parasite in nonhuman primates, is a cosmopolitan nematode known to infect over 35 million people worldwide [Ryan and Ray, 2010] and was found in 15% of primates in the Sabangau. Strongyloidiasis is the resultant chronic disease that can become highly pathogenic and fatal in non-human primates and humans [Bangs et al., 2006; DePauli and Johnson, 1978) and has even been identified as the main cause of death in orangutans in captivity [Foitova et al., 20091.

One surprising finding was that of the presence of the Entodiniomorph ciliate *Troglodytella abrassarti* in gibbon samples and half of all orangutan samples. These ciliate protozoa reside in the hindgut of herbivorous mammals and actively participate in digestion aiding the breakdown of cellulose, fibre and starch [Collet et al., 1984; Profousová et al., 2011]. Several entodiniomorphid genera have been recovered from apes although these are usually restricted to Africa [Collet et al., 1984; Howells et al., 2011; Kaur et al., 2010; Pomajbíková et al., 2010] for example high abundance of T. abrassarti (81% of samples) recovered from gorillas in the Central African Republic [Freeman et al., 2004]. The presence of these ciliate in the gut flora of primate populations suggests possible symbiosis with detection recently acknowledged as a viable measure of individual health [Modry et al., 2009; Tokiwa et al., 2010]. This is the first published occurrence of this ciliate species in wild gibbons and orangutans. Other reported hosts include black and white colobus [Profousová et al., 2011], hamadryas baboons [Howells et al., 2011], captive siamangs [O'Donohue et al., 1993] Kloss gibbons and orangutans [Mortelman et al., 1971). Interestingly, apes captured from the wild and fed on unsatisfactory diets soon lose their intestinal fauna of Troglodytella sp. [Stahl 1984]. Fluctuations in ecological factors are also likely to disrupt the micro-organism balance of a healthy host. Langurs have a specialised compound digestive anatomy with a distinctive range of microbial symbionts in comparison to other primates with simple gut arrangements [Chivers, 1994]. As the langurs in this study lacked this ciliate, we can infer that they may not be viable hosts and that diet may therefore play a role in protozoa abundance.

Diet and Nutrition

The greater prevalence of protozoa recorded for the langurs may be explained by nutritional intake, as the ability to cope with parasite infections is connected to host nutritional status [Coop and Holmes, 1996; Coop and Kyriazakis, 1999] with overall host resilience being augmented by greater dietary quality [Kyriazakis and Houdijk 2005]. We found a positive correlation between level of folivory and the number of infected individuals harbouring protozoa, which could be explained by the simple transmission route of protozoa such as Entamoeba hystolytica/dispar via meta-cysts in contaminated food or water or encysted on foliage, possibly ingested in higher quantities by the langurs. In comparison to their more frugivorous neighbours colobines have a greater reliance on plant matter to meet their nutritional requirements and thus have to consume greater quantities of food [Davies et al., 1988; Waterman and Kool, 1994], potentially increasing their chances of consuming infective-stage parasites [Boissier et al., 1999]. Percentage of leaves in the diet was also associated with a higher PSR and coinfection of both protozoa and helminths, suggesting a relationship between folivory and langurs' greater infection of parasites than the other sympatric species in this population. Another consideration is that greater insectivory may increase a host's chances of ingesting vector-borne parasites, supported by the orangutan's greater dietary composition of invertebrates and greater helminth prevalence.

Although we cannot simply assume that overlap in diet results in feeding competition, it can be used as a useful measure for potential inter-specific competition [Marshall et al., 2009b: Schoener, 1982]. Orangutan diets overlap with gibbon's in the Sabangau by 69% [Cheyne, 2010]. Marshall (2009b) also found a large dietary overlap between orangutans and gibbons. Orangutans, classified as frugivores and opportunistic feeders [Wich et al., 2009] have been shown to be capable of digesting highly fibrous material, with efficient fermentation due to their naturally proactive gut micro-flora [Schmidt et al., 2005]. They regularly go through periods of prolonged energy balance and regularly rely on large quantities of fall-back foods for survival [Constantino and Wright, 2009; Marshall et al., 2009a; Harrison et al., 2010] which may reduce immune responses and subsequently elevate parasite burdens during these periods.

Home Range

Ranging behaviour is fundamentally governed by spatial and temporal resource availability [Clutton-Brock and Harvey, 1977; Isbell, 1991]. Temporal availability of fruit directs not only the activity budget and feeding strategy of orangutans [Morrogh-Bernard et al., 2009], but more importantly density and subsequent carrying capacity [Morrogh-Bernard et al., 2003; Wich et al., 2004a]. Peat-swamp forests have regular fruit availability even in lower productivity regions, in contrast to mast-fruiting forests such as those dominated by dipterocarp tree species which show greater fluctuation in fruit availability. This results in a greater day range and foraging budget in peat-swamp forests, thus increasing likeliness of interspecific encounters and consequent parasite spread.

Nunn and Dokey [2006] found that increased intensity of range use resulted in an increase in parasite levels. Labes and colleagues [2009] also identified ranging patterns as the most important parameter for infection risk in captive, semi-captive and wild orangutans. Orangutans, particularly flanged males, are known to have very large ranges thus increasing likeliness of increasing infection probability [MacKinnon, 1974]. Our data detract from this finding, and suggest the effect of increased ranging is masked by other factors, as orangutans had the largest range but lowest PSR. However, this ranging behaviour could therefore be responsible for increased helminth prevalence as more individuals are exposed to infected individuals across a wider spatial area.

Body Size

Large body size or weight is associated with PSR due to its positive correlation with body surface, longevity and metabolism [Arneberg, 2002; Morand and Poulin, 1998; Vitone et al., 2004). Further to this, body size may represent a proxy measure for age [Pettifer, 1984] with variation in susceptibility throughout the host's life. Our data do not support either of these predictions, as langurs had the highest PSR yet are overall the lightest primate species [Oates et al., 1994] and there appeared only marginal differences between age categories. However, the greater output of helminths, which are themselves comparatively much larger than protozoa, does correlate with the orangutans' larger size as would be expected. Conferring to the predictions of epidemiological theory, group size and population density may provide more favourable indices as hosts act as multiple patches of habitable environment [Morand and Poulin, 1998]. With more potential hosts present a similar cumulative effect as increasing body size occurs, further amplified by overlap of other host species as presented in this study.

Group Size

This study supports previous evidence that larger host group size is likely to increase infection risk due to greater contact and pathogen exposure [Freeland, 1976; Vitone et al., 2004]. Larger groups were associated with higher protozoa prevalence and diversity of parasite assemblages. Group size, as a major component of social organization, may be a contentious index for orangutans as they spend the majority of their time individually or with offspring [Galdikas, 1988; van Schaik, 1999], but are known to be social with a dominance hierarchy organised around the dominant flanged male [Mitra-Setia et al., 2008]. A wide variety of mechanisms interact with group size and disease risk [Nunn and Altizer, 2006] and as social contact is still maintained between orangutan individuals, we propose that regional population density is a clearer indicator of transmission potential.

Population Density

Most of the variation in parasite prevalence and species richness between and within taxa of primates and parasites reported in this study may be explained by

population density. In a broad-scale comparative study encompassing 941 parasite-host combinations in 101 anthropoid primates, Nunn et al. [2003] found that after testing for a wide range of socioecological parameters, PSR correlated most significantly with host population density. This is supported by numerous authors [Anderson and May, 1979; Arneberg, 2002; Chapman et al., 2005a; Mbora and McPeek, 2009]. According to ecological theory, density of a given species correlates positively with food availability [Cant, 1980; Pianka, 1974] and is limited in primate species with slow life histories by fluctuations in periods of food shortages, as in the case of orangutans [Marshall and Leighton, 2006; Marshall et al., 2009a). Density compensation results in a decline in abundance of competing species thus resulting in increased density of the other species. Following this, primate population densities tend to decrease following disturbance [Fuller et al., 2009; van Schaik et al., 1995] but localised densities may increase due to habitat fragmentation [Mammides et al., 2009; Marsh, 2003; Mbora and McPeek, 2009] thus exacerbating confined parasite transmission. Understanding the connection between primate densities and disease transmission is therefore essential for assessing threats of primates facing substantial anthropogenic disturbance.

Sociality

Severe population declines have been attributed to outbreaks of disease spread through social contact, for example with an epidemic of an unknown pathogen in siamangs (Symphalangus syndactylus) [Palombit, 1992]. One marked difference between the study species are characteristics of their social organisation. Gibbons at this site spent 87% of their time together socially [Cheyne, 2010], whereas orangutans tend to have far less exchange with other individuals, spending just 18% of their time in social interactions [Morrogh-Bernard et al., 2009]. Conversely, gibbons also reduce the potential for direct contact with other groups via territorial encounters by singing [Brockelman, 2009; Raemakers 1979] and group encounters or fight occurrences were relatively low as a result of larger territories and lower densities [Cheyne, 2010]. This may reduce likely encounters and subsequently lower encounter frequency related to parasite transmission probability. Adult male orangutans also adopt a similar strategy by use of their distinctive long calls, which can travel several kilometres across the forest [Galdikas, 1983], consistent evidence of which points to an intra-sexual spacing function [Mackinnon 1974; Mitani,

1985]. Red langurs have a uni-male social system with a polgynous mating system in groups of 2 -13 individuals with overlapping ranges [Supriatna, 1986]. Together with male dispersal and frequent challenges from solitary males [Davies, 1987] langur sociality may subsequently increase pathogen spread via mechanisms described earlier.

Gibbons harboured the lowest variety and prevalence of parasites yet are known to be highly social. In the Sabangau Gibbons spent 24% of their of their social time playing and 35% allo-grooming [Cheyne, 2010] which although may act as a function for reducing ectoparasites in addition to social cohesion [Hutchins and Barash, 1976], is likely to increase pervasiveness of horizontally transmittable pathogens. However, although this may account for the spread of parasites between conspecifics, it doesn't appear to exacerbate their parasite burdens to that of the levels of the langurs. Many questions remain in epidemiology regarding the role that sociality and behaviour have on the spread of infectious disease.



Fig. 8. Inter-specific interactions between gibbons, langurs and orangutans representing: (a) dietary overlap (expressed as % shared food species eaten) and (b) encounter rate (expressed as % of total inter-specific interactions).

Source: Marshall 2009b; Cheyne 2010. * = data deficient.

Inter-specific Competition

The effects of living in sympatry with other primate competitors may have profound influence on the behavioural ecology of primate species and therefore the risk of exposure to pathogens. Ecological theory implies that no two species occupy the same niche [Cant, 1980; Pianka, 1974]. Niche differentiation is clear in peat-swamp forest, with gibbons adapting well to exploiting lowproductivity forest. Gibbons occupy a specialized adaptive zone due to their superior adaptation of brachiation, terminal branch feeding and frugivory [Grand, 1972; Michilsons et al., 2009], illustrated by the typical lack of sympatry between different gibbon species [Brockelman, 2009; although see Geissmann, 1991]. Gittins [1982] study of *H. agilis* in Malaysia describes a different activity start time to *H. albibarbis*, which may possibly be attributed to the effects of resource competition as that field site is lacking orangutans, one of the main competitors of gibbons [Marshall, 2010]. Cheyne (2010) also points to feeding overlap with orangutans, recorded as 69% [Figure 8], as a likely causal determinant of variability in sleeping and waking behaviour in the gibbons in order to minimise competition. The majority of interspecific encounters of gibbons are with orangutans [32% of all aggressive encounters] and involving feeding sites. In Marshall's [2009b] study of competition and niche overlap in gibbons. he observed that during periods of food scarcity the overlap of gibbon diets with langurs and orangutans was reduced. This suggests diversification in fall-back feeding strategies which will inevitably rise in importance as disturbance becomes greater and food becomes scarcer, culminating in fluctuations in ability to deal with parasite infections. Marshall also reported a 27% overlap in diet overlap between langurs and gibbons but found that habitat selection was not used as a strategy to reduce this potential feeding competition. The relatively high rate of cross-species interaction has implications for the transmission potential of many of the parasites described in this study, calling for more comprehensive long-term assessments on the mechanisms of pathogen spread between sympatric primate species.

Environment & Disturbance

Strata use may also be a determinant in the levels of parasites found in this study. Both langurs [Davies and Baillie, 1988] and orangutans are known to frequent the ground in search of shoots or termites [Morrogh-Bernard et al., 2009] which may potentially expose them to greater numbers of infectious stage generalist parasites [Nunn and Altizer, 2006] Hookworm were found to be the most common helminth infecting all three primates in this study, with orangutans having the greatest output and prevalence. Fertilised females release up to 20,000 eggs daily, which hatch within 48 hours of reaching the soil surface. Rhabditiform larvae molt to become filariform (infective) larvae which are able to survive up to 6 weeks in conditions characterised by those present in this study [Roberts and Janovy, 2008; Ryan and Hay, 2010]. This resilient life cycle is also shown in the second most common helminth Ascaris lumbricoides which is highly resistant to environmental conditions and may remain viable for up to 6 years in mild climates, therefore having implications for infection probability between the three primate species. The distinctive conditions present in peatswamp forests such as high soil PH and leaf litter offer an array of environmental or host-extrinsic factors for infective stages of parasites and their intermediate and final hosts. Further research into how these characteristics affect parasite-host relationships, including meta-analyses across various sites would enable greater understanding of pathogen spread within this habitat in comparison to other forest types.

Ecological stress in primates has been attributed to competition from other species and is often linked to anthropogenic disturbance [Daszak et al., 2001; Gillespie et al., 2005b; Sleeman et al., 2000]. Chapman and colleagues [2006] found that stress has a synergistic effect on parasitism by weakening the immune system, supported by known links between stress and infections of Balantidium coli [Anargyrou et al., 2003; Schuster and Ramirez-Avila, 2008]. These pathogenic flagellates occurred in almost half of the population of langurs in this study, yet marginal in the gibbons and absent in the orangutans, thus indicating stress as a possible determinant of the infection levels of these pathogenic protozoa. Possible contamination between the natural reservoirs forest-dwelling pigs and also humans are important considerations for transmission potential [Schuster and Ramirez-Avila, 2008]. The relatively high overall prevalence and large diversity of parasites of these primate species suggest a possible outcome of disturbance. The Sabangau has been subjected to consistent uncontrolled illegal logging with increased severity and frequency of fire due to large-scale drainage of peatswamp, with ramifications spreading throughout the ecosystem. These include changes in primate behaviour [Cheyne, 2007] conceivably exacerbating stress and subsequent parasite infections.

Interestingly, our results are in support of a recent comparative study on global parasite patterns in primates [Altizer et al., 2007]. The investigation compared threat status with parasite richness and revealed that counter to predictions, the most threatened taxa harboured lower parasitic diversity (mean 15%) when compared to nonthreatened species (mean 19%). This suggests that disturbance and host characteristics that increase extinction risk may also lead to the loss of parasites. Hosts are expected to outlive their parasites, especially those that live uniquely on endangered mammal species [Gompper and Williams, 1998]. Kamilar and Paciulli [2008] found that across the primate order, folivores appear more resilient to disturbance than their more frugivorous counterparts, which may have a distinct connection with strategies for reducing disease transmission during periods of stress.

With our assessment of the parasite communities of three species of primates inhabiting a peat-swamp forest, we found langurs to have a total greater output, PSR and overall prevalence than orangutans and gibbons. We attribute greater population density to the greater parasite burdens found, with higher percentage of leaves and flowers in the diet and small average body size also playing a significant role. Our investigation points to likely connections between elements of primate socioecology and parasitism, however more comprehensive long-term surveillance is necessary to fully understand these dynamics. We suggest further investigations focus on the ecological mechanisms between host density and pathogen transmission. Our study recognises a high level of overlap in parasite assemblages highlighting the potential for pathogen transmission, calling for more comprehensive research of the patterns of gastro-intestinal parasites and the influence of sympatry on inter-specific disease spread.

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Chapter Five – Synthesis

This research was developed upon the foundation of my previous knowledge and experience of primate ecology, conservation and parasitology. However, I wasn't yet acutely aware of the profound complexity and fundamental importance of parasites in ecosystem function or their role as indicators of health and subsequent importance for primate conservation. The development of this thesis has facilitated my deeper reverence for all organisms, from which I hope I have provided a solid argument in Chapter 3 for the incorporation of all elements throughout the ecosystem within biodiversity health assessments.

As we investigated in Chapter 4, the dynamics of parasite-host relationships and transmission trends are the consequence of many mechanistic links interacting with one another. The results presented in this research point to a distinct series of factors that are most likely to have the principal influence on the prevalence and diversity of parasites occurring in the Sabangau primates. I have identified these key variables as: nutritional intake, group size and population density. With regards to describing the parasite communities reported in this study, these variables act as potential proximate causes. In order to complete a more rigorous understanding of these relationships we must also consider the ultimate causes of the variation. The most prominent of these is that of resources availability: all socioecological interactions will be affected by an immunocompromised individual with a scarcity of food resources, as will the ability to deal with infection. Availability and spatial distribution of food are key components in governing ranging behaviour, density and behaviour of primates with nutritional status governing reproduction, mortality and stress in most primate species. Resources are provided by the environment, so assessment of these levels and understanding their effects on the health and survival of primates has fundamental implications for conservation management.

Ecological monitoring programs are essential for the preservation of forests and biodiversity. Largely due to ongoing work conducted in the Sabangau, the PSFs of Borneo are now recognised as incredibly important primate habitat, for carbon storage, biosequestration and ecosystem services. Further contribution to their preservation will have many benefits to local people who rely on this unique biome. To conserve, we must first understand the ecological interactions of this greatly understudied habitat, especially parasite dynamics and the risks of EID for the survival of wild animal populations. However, many more questions remain unanswered and there is a pressing need to gain more support for preservation of regions.

It seems a recurrent theme of articles concerning awareness of pathogen's role in conservation that the threat of EID should be recognised as increasing exponentially as human populations expand to extreme levels. Current trends of deforestation in Borneo evoke images of a bleak outlook for the future of its beautiful habitat (Figure 9). Loss of habitat may lead to fragmentation and subsequent crowding of small populations, thus increasing host densities in smaller geographical regions. Our study supports previous evidence that density is positively correlated with increases in parasite richness and prevalence. As human-dominated ecosystems become increasingly common, crop-raiding and other interactions by primates and other animals becomes an integral aspect of their ecology consequently growing in significance as a human-wildlife concern. This also raises concern for health as described in Chapter 3 due to potential disease transmission between humans and NHPs.



Figure 9. Forest loss in Borneo from 1950 – 2010 and projected loss by 2020 if following current trends. Source: Nelleman et al. 2007.

With this research I argue that parasites should be paid greater attention in light of their significance in ecosystem function and disease transmission. Parasites are important drivers for biodiversity as they control host population dynamics, interspecific competition and influence energy flows. I have provided evidence of their complexities within ecosystems and their influence of host and population health, and I hope to contribute to our understanding of disease transmission dynamics for the benefit of primate communities, other wildlife and humans.

Chapter Six - Conclusions and Recommendations

This research directs us towards two distinct conclusions disseminated from the results and discussion based upon my initial questions and the focus for each article presented.

1. Parasitism may be a useful index for assessing health of a population of primates, and should be subsequently adopted in bio-monitoring programs and ecological surveys.

2. Inter-specific interactions and variation in socioecological factors play a central role in transmission of parasites, with population density highlighted as a significant determinant of potential spread.

6.1 Specific Conclusions

- Much remains to be explored in this vast and highly important area of research, particularly as changing environmental conditions are likely to influence potential pathogen spread.
- Niche overlap increases chance of pathogen transmission.
- Long-term surveillance of parasite communities across a wide range of primate hosts is essential to identify potential disease transmission.
- Parasites act as valuable non-invasive indicators of individual, population and ecosystem health.
- Simple correlations (R_s) are useful measures of the substantive importance of an effect, but cannot be used to directly claim causal relationships. This test provided a logical connection between socioecological variables; however more detailed analyses from long-term parasite surveillance will be valuable to understand these relationships in greater depth.
- Minimum sample size was ascertained for statistical analyses. However, future studies will benefit from a larger sample size of more individuals, from additional groups across a series of comparative study sites.

6.2 Recommendations

In addition to these conclusions, I present a number of recommendations below based on an amalgamation of what we know from previous research, the current study and primate threats.

- Recognition by all biologists, ecologists and conservationists that parasites play an integral role in ecosystem function.
- Greater incorporation of health monitoring into primate action plans and biomonitoring programs.
- Monitor fluctuations over time and responses to environmental change using appropriate indicators in order to accurately predict how anthropogenic change may affect pathogen spread.
- Full epidemiological assessments encompassing humans in proximity to study species.
- Call for standardization of techniques in field and laboratory methods used in primatology and parasitology (see Gillespie 2006; Howells et al. 2011; Setchell & Curtis 2011).
- Primate-parasite research to be viewed as a principal component, along with resource competition and predation, to be incorporated into an integrative framework for primate socioecology.

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Appendices

Appendix I. Health & Safety & Animal Ethics

Health and Safety

Coprological research requires the direct handling of faecal matter and therefore pertains to a certain degree of risk to health. Every effort was made to minimize the risk of transmission of parasitic infection to all people involved in the collection and processing of samples. Surgical mask and latex gloves were worn by those involved at all times in this process and when in close vicinity to the primates which prevented the chances of zoonotic transmission or any negative impacts on the primate's health. When following the primates, awareness was maintained with regards to keeping a safe distance and not to display threatening behaviours towards the primates.

Ethics

When following the primates, awareness was stressed about keeping a safe distance and not to display threatening behaviours towards the primates. Although hunting is not a major concern at this site, all project members acknowledge that habituation can increase hunting vulnerability, and paths were kept to a minimum. The local communities received economic benefits including employment, and any chances of negative impacts are minimized. The project methods did not include any handling of animals.

20th April 2011

Animal Ethics Acknowledgement

I hereby confirm that although my project includes working in the vicinity of wild animals, there will be no direct contact with any individuals at any point and all indirect ethical issues have been taken into consideration and any potentially adverse effects of the data collection minimized in all circumstances.

When following the primates, awareness will be stressed about keeping a safe distance and not to display threatening behaviours towards the primates. Although hunting is not a major concern at this site, all project members acknowledge that habituation can increase hunting vulnerability, and paths will be kept to a minimum. The local communities will receive economic benefits including employment, and any possibility of negative impacts will be minimized. The project methods do not include any handling of animals.

Signed,

Harry Hilser

Appendix II. General Ethics Clearance

Section I: Applicant Details

1.	Name of Researcher (applicant):	HARRY HENRY BENJAMIN HILSER
2.	Status (please click to select):	Other
3.	Email Address:	hhilser@yahoo.com
4a.	Contact Address:	6 AWGAR STONE ROAD, HEADINGTON, OXFORD, 0X3 7FD. UK
4b.	Telephone Number:	(+44) 7725554619

Section II: Project Details

5. Project Title:		An Assessment of Primate Health in the Sabangau Peat-Swamp Forest,
		Central Kalimantan, Indonesian Borneo

Section III: For Students Only:

6.	Module name and number	P20107 - FINAL PROJECT
7.	Supervisor's or module leader's name:	DR SUSAN CHEYNE
8.	Email address:	susan.cheyne@zoo.ox.ac.uk
9.	Contact address:	Susan M. Cheyne BSc (Hons) PhD CBiol MIBiol
		Director Sabangau Gibbon and Felid Behaviour Project,
		Orang-utan Tropical Peatland Project,
		Wildlife Conservation Research Group,
		Department of Zoology, University of Oxford.
		Tubney House, Abingdon Road,
		Tubney, OX13 5QL, UK.

Supervisor: Please tick the appropriate boxes:

\square	The student has read the University's Code of Practice
\square	The topic merits further research
\square	The student has the skills to carry out the research
	The participant information sheet or leaflet is appropriate
\square	The procedures for recruitment and obtaining informed consent are appropriate

Comments from supervisor:

HARRY IS FAMILIAR WITH WORKING IN REMOTE ENVIRONMENTS AND HAS PAST EXPERIENCE OF THIS WORK. THIS STUDY WILL NOT INVOLVE WORKING WITH HUMANS

Section IV: Research Checklist

Please answer each question by ticking the appropriate box:

		YES	NO
1.	Does the study involve participants who are particularly vulnerable or unable to give informed consent? (e.g. children, people with learning disabilities, your own students)		
2.	Will the study require the co-operation of a gatekeeper for initial access to the groups or individuals to be recruited? (e.g. students at school, members of self-help group, residents of nursing home)		
3.	Will it be necessary for participants to take part in the study without their knowledge/consent at the time? (e.g. covert observation of people in non-public places)		
4.	Will the study involve discussion of topics which the participants would find sensitive (e.g. sexual activity, own drug use)?		
5.	Are drugs, placebos or other substances (e.g. food substances, vitamins) to be administered to the study participants or will the study involve invasive, intrusive or potentially harmful procedures of any kind?		
6.	Will blood or tissue samples be obtained from participants?		
7.	Is pain or more than mild discomfort likely to result from the study?		\square
8.	Could the study induce psychological stress or anxiety or cause harm or negative consequences beyond the risks encountered in normal life?		
9.	Will the study involve prolonged or repetitive testing?		
10.	Will financial inducements (other than reasonable expenses and compensation for time) be offered to participants?		
11.	Will the study involve recruitment of patients or staff through the NHS?		\square

Signed: . .

..... Principal Investigator

Signed: -

..... Supervisor or module leader (where appropriate)

Appendix III – Parasite Life Cycles

As we explored in Chapter 1, the life cycles and transmission routes of parasites are important considerations for spread between primate hosts. I include here this information for the top two most common helminth and protozoa parasites recovered from my research.

Enterobius vermicularis



Eggs are deposited on perianal folds $\mathbf{0}$. Self-infection occurs by transferring infective eggs to the mouth with hands that have scratched the perianal area $\mathbf{0}$. Person-to-person transmission can also occur through handling of contaminated clothes or bed linens. Enterobiasis may also be acquired through surfaces in the environment that are contaminated with pinworm eggs (e.g., curtains, carpeting). Some small number of eggs may become airborne and inhaled. These would be swallowed and follow the same development as ingested eggs. Following ingestion of infective eggs, the larvae hatch in the small intestine $\mathbf{0}$ and the adults establish themselves in the colon $\mathbf{0}$. The time interval from ingestion of infective eggs to viposition by the adult females is about one month. The life span of the adults is about two months. Gravid females migrate nocturnally outside the anus and oviposit while crawling on the skin of the perianal area $\mathbf{0}$. The larvae contained inside the eggs develop (the eggs become infective) in 4 to 6 hours under optimal conditions $\mathbf{0}$. Retroinfection, or the migration of newly hatched larvae from the anal skin back into the rectum, may occur but the frequency with which this happens is unknown.



Eggs are passed in the stool \bigcirc , and under favorable conditions (moisture, warmth, shade), larvae hatch in 1 to 2 days. The released rhabditiform larvae grow in the feces and/or the soil \bigcirc , and after 5 to 10 days (and two molts) they become filariform (third-stage) larvae that are infective \bigcirc . These infective larvae can survive 3 to 4 weeks in favorable environmental conditions. On contact with the human host, the larvae penetrate the skin and are carried through the blood vessels to the heart and then to the lungs. They penetrate into the pulmonary alveoli, ascend the bronchial tree to the pharynx, and are swallowed \bigcirc . The larvae reach the small intestine, where they reside and mature into adults. Adult worms live in the lumen of the small intestine, where they attach to the intestinal wall with resultant blood loss by the host \bigcirc . Most adult worms are eliminated in 1 to 2 years, but the longevity may reach several years.

Some A. duodenale larvae, following penetration of the host skin, can become dormant (in the intestine or muscle). In addition, infection by A. duodenale may probably also occur by the oral and transmammary route. N. americanus, however, requires a transpulmonary migration phase.

Entamoeba histolytica/dispar



Cysts and trophozoites are passed in feces ①. Cysts are typically found in formed stool, whereas trophozoites are typically found in diarrheal stool. Infection by *Entamoeba histolytica* occurs by ingestion of mature cysts ③ in fecally contaminated food, water, or hands. Excystation ③ occurs in the small intestine and trophozoites ④ are released, which migrate to the large intestine. The trophozoites multiply by binary fission and produce cysts ④, and both stages are passed in the feces ④. Because of the protection conferred by their walls, the cysts can survive days to weeks in the external environment and are responsible for transmission. Trophozoites passed in the stool are rapidly destroyed once outside the body, and if ingested would not survive exposure to the gastric environment. In many cases, the trophozoites remain confined to the intestinal lumen ($\underline{\Box}$: noninvasive infection) of individuals who are asymptomatic carriers, passing cysts in their stool. In some patients the trophozoites invade the intestinal muccos ($\underline{\Box}$: intestinal disease), or, through the bloodstream, extraintestinal sites such as the liver, brain, and lungs ($\underline{\Box}$: extraintestinal disease), with resultant pathologic manifestations. It has been established that the invasive and noninvasive (erythrophagocystosis). Transmission can also occur through exposure to fecal matter during sexual contact (in which case not only cysts, but also trophozoites could prove infective).



Cysts are the parasite stage responsible for transmission of balantidiasis \bigcirc . The host most often acquires the cyst through ingestion of contaminated food or water O. Following ingestion, excystation occurs in the small intestine, and the trophozoites colonize the large intestine O. The trophozoites reside in the lumen of the large intestine of humans and animals, where they replicate by binary fission, during which conjugation may occur O. Trophozoites undergo encystation to produce infective cysts O. Some trophozoites invade the wall of the colon and multiply. Some return to the lumen and disintegrate. Mature cysts are passed with feces O.

Life cycle image and information courtesy of DPDx.

Appendix IV – Parasite Images, Pathogenicity and Transmission

Parasite Name	Transmission	Pathogenicity	Image
<i>Enterobius vermicularis</i> (Pinworms)	More common in females and children and in temperate regions. Eggs resistant and highly infective.	Most widespread and prevalent pathogenic nematode in the world. No significant pathology induced.	50μm
Hookworm sp. (<i>Ancylostoma/ Necator</i> spp.)	Eggs hatch in soil and mature to rhabditiform larvae that molt to produce infective filariform larvae; penetrates skin and migrates to gut.	Causes epithelium lesions resulting in malabsorptive syndrome. High rates of blood loss; larvae may stay in host up to 14 years.	Бо µт
<i>Trichuris trichuria</i> (Whipworms)	Associated with soil defecation and spread by infective eggs. Can withstand extreme desiccation.	Colonic ulceration of gut lumen can also open infection to bacteria. Effects 1billion people worldwide.	Б оµт
<i>Strongyloides</i> sp.	Infective filariform larvae free- living in environment; entry through skin and migration through organs.	Potentially highly pathogenic in humans and NHPs. Causes epithelium lesions resulting in malabsorptive syndrome. Responsible for majority of deaths of orangutans in captivity.	Б оµт
Ascaris lumbricoides	Ingestion of embryonated eggs in soil. Prevalent in tropical climates.	This organism is a clearly defined pathogen in humans with infection rates as high as 45% in Central and South America. May be highly symptomatic if host immuno-compromised.	бо ра
<i>Trichostrongylus</i> sp.	Ingestion of infective stage larvae from infected food.	Mildly pathogenic but often asymptomatic.	50μm
Schistosoma mansoni	Life cycle requires intermediate snail host. Found in freshwater environments; infective cercariae penetrate skin.	Second only to malaria in terms of most devastating disease. Effects over 200 million people worldwide. Causes debilitating and even fatal bilharzia.	50μm

Carly .

Helminth Parasites Recovered

Protozoan Parasites Recovered

Parasite Name	Transmission	Pathogenicity	
<i>Entomoeba coli</i> cyst	Faecal/ oral or contaminated food or water.	Least pathogenic, typically commensal. Most common amoeba found in humans and NHPs.	10 μm
Entamoeba histolytica/dispar	Direct transmission between individuals or ingestion of infective cysts.	<i>E. histolytica</i> and <i>E. dispar</i> indistinguishable morphologically. Although <i>E. dispar</i> is non-pathogenic, <i>E. histolytica</i> can cause severe amoebiasis so detection is treated as a complex of the two.	ο 10 μr
Blastocystis hominis	Faecal/ oral or contaminated food or water.	Still uncertain as to pathogenic level but some links with disease as potential agent.	<u>[10 µп</u>
<i>Balantidium coli</i> trophozoite	Faecal/ oral or contaminated food or water. Goats and humans act as common reservoirs for infection.	Only pathogenic ciliate known in humans. Can be pathogenic and may cause severe physical debilitation in primates.	Σ 50 μη
<i>Balantidium coli</i> cyst	(as above)	(as above)	50 μη

Appendix V – Cover Letters for Article Submission

1. American Journal of Primatology

Editorial Board American Journal of Primatologists

5th September 2011

Harry Hilser 6 Awgar Stone Road, Headington, Oxford, Oxfordshire. OX3 7FD Tel: 07725554619 Email: hhilser@yahoo.com

Dear Sirs,

Please find accompanying this letter submission of manuscript titled:

'Socioecology and Gastro-Intestinal Parasites of Sympatric Primate Species Inhabiting the Sabangau Peat-Swamp Forest, Central Kalimantan.'

The parasite communities of wild red langurs and gibbons are as of yet unreported. With this research we assess parasitism in three primate species inhabiting a region of profound importance for these primates and other biodiversity, and provide insight into transmission dynamics and socioecological interactions.

Word Count: 5,507

I declare that it is original work, that it is not being submitted elsewhere, that all authors agree with the contents and to the submission for publication, and all appropriate ethics and other approvals were obtained for the research. All co-authors acknowledge their participation in conducting the research leading to this manuscript and all agree to its submission to be considered for publication by AJP.

I look forward to hearing from you,

Yours faithfully,

Harry Hilser



Harry Hilser – Dissertation 2011







1. Biotropica

Editorial Board **Biotropica Journal**

Harry Hilser 6 Awgar Stone Road, Headington, Oxford, Oxfordshire. OX3 7FD Tel: 07725554619 Email: hhilser@yahoo.com

5th September 2011

Dear Sirs.

Please find accompanying this letter submission of manuscript titled:

^CCreating Connections: Integrating Health Monitoring Into Primate Conservation Management'

The recent emergence of new paradigms for successful conservation programs has sparked a discussion as to how to implicate monitoring programs and assess health of biodiversity. Using the appropriate example of primates and their parasites, we argue that monitoring individual, population and ecosystem health is the key to achieving conservation management goals. Cohesion with all stakeholders and publication is an essential facet. We illustrate with examples from our field site in Borneo that by using key indicators throughout all levels in the ecosystem these monitoring efforts are maximised. This Commentary provides a platform for forum discussion and encourages adoption of specific techniques and approaches relevant to all biodiversity research and conservation in tropical rainforests.

Word Count: 1.757

I declare that it is original work, that it is not being submitted elsewhere, that all authors agree with the contents and to the submission for publication, and all appropriate ethics and other approvals were obtained for the research. All co-authors acknowledge their participation in conducting the research leading to this manuscript and all agree to its submission to be considered for publication by Biotropica.

I look forward to hearing from you,

Yours faithfully,

Harry Hilser









MSc Primate Conservation