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Bird-parasite dynamics in a Bornean rainforest: the effects of selective logging and host characteristics

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Abstract

Parasites are a natural and integral part of all ecosystems, but human disturbance could potentially negatively affect the host-parasite dynamics. Selective logging is considered one of the major threats to forest biodiversity in Southeast Asia, but how does logging affect avian-parasite dynamics? I investigated avian ectoparasites and blood parasites in primary and logged forest sites in Northeast Borneo, Malaysia, and tested whether parasite infestation intensity or prevalence differed between habitat types, the species- and trait-specific variation of parasite infestation within the avian community, and the connection between avian parasite infestation and avian body condition. There were overall little difference between forest types in intensity and prevalence of avian parasites, and no correlation of avian parasites and the body condition indices. Infection of blood parasites was slightly positively correlated to higher intensity and prevalence of ectoparasites, indicating that initial infection could increase the susceptibility of multiple infections. There were evidential differences within intensity and prevalence between species, families, and trait groups, highlighting the importance of detailed ecological knowledge of the study system to predict the effect of habitat alteration. That only a few significant forest type interactions were found, is likely an effect of the limited sample sizes and highly aggregated distribution of parasites. The changes in intensity and prevalence of avian parasites and the implications for the avian community following logging remain difficult to predict, as host-parasite systems are complex and subject to many uncontrolled variables. However, the results indicate that selectively logged forest and primary forest are very similar with regards to the ecological factors affecting the avian-parasite dynamics of the tropical forests in Borneo.

Sammendrag

Parasitter er en naturlig og omfattende del av alle økosystemer, men menneskelige forstyrrelser kan potensielt påvirke dynamikken mellom vert og parasitter negativt. Selektiv hogst er ansett som en av de største truslene mot biodiversiteten i Sørøst Asias skoger, men hvordan vil hogst påvirke fugleparasittene? Jeg undersøkte ektoparasitter og blodparasitter hos fugl i primærskog og hogstskog i nordøst-Borneo, Malaysia, og testet om intensitet eller prevalens av parasitter var ulik i disse to habitatene, og om parasitter kunne kobles til kondisjon og ulike økologiske og funksjonelle trekk ved fugler. Det var liten forskjell mellom skogstypene i intensitet og prevalens av fugleparasitter, og ingen korrelasjon mellom fugleparasitter og fuglenes kondisjon. Infeksjon av blodparasitter var svakt positivt korrelert med høyere intensitet og prevalens av ektoparasitter, noe som kan antyde at primærinfeksjoner kan lede til flere infeksjoner. De tydelige forskjellene i intensitet og prevalens av parasitter mellom arter, familier og funksjonelle grupper viser at detaljert økologisk kunnskap om artene og systemet undersøkt er viktig for å kunne avgjøre potensiell effekt av habitatendringer. At bare noen få signifikante forskjeller mellom skogstyper ble funnet er sannsynligvis forårsaket av det begrensede antallet individer målt i hver artsgruppe og de svært aggregerte distribusjonene av parasitter. Endringer i intensitet og prevalens av fugleparasitter og implikasjonene for fuglesamfunnet i sin helhet som følge av hogst forblir vanskelige å forutse, ettersom vert-parasitt systemer er komplekse og avhengige av mange ukontrollerbare variabler, men resultatene indikerer at hogstskog og primærskog i tropiske skoger i Borneo er svært like med tanke på de økologiske faktorene som påvirker dynamikken mellom fugler og deres tilhørende parasitter.

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1. Introduction

1.1 Tropical forests, logging and parasites

Tropical forests comprise some of our most species rich areas, supporting approximately 50% of all described species (Dirzo & Raven 2003; Wright 2005). The areas under forest cover is continuously decreasing due to land conversion, while the forests left standing are increasingly being transformed from primary forest to logged degraded forest. It is estimated that about 17% of the global forest cover has been lost since 1850, with most of the loss occurring in the tropics after 1950 (Houghton 1999). The rate of deforestation in the tropics does not seem to be slowing (Laurance et al. 2012; Sodhi et al. 2004a).

The loss and degradation of forests leads to direct and indirect effects on the forest's flora and fauna. Infectious pathogens and parasites may increasingly contribute to the decline of populations of host species by altered prevalence and severity of infections, as the quality and quantity of forests declines (Brearley et al. 2013). With over 20,000 terrestrial parasites described (Poulin 2011), and an unknown number of undescribed species, the potential impact on biodiversity may be substantial. Southeast Asia has a rich avifauna, with a high number of endemic and threatened species (Sodhi et al. 2006). The effect of logging on parasite and pathogen dynamics and interactions within the avian community is thus of high importance for conservation. However, our knowledge of the influence of human induced changes, such as logging, on the prevalence of wildlife diseases and parasites is meagre (Brearley et al. 2013).

1.2 Parasites – an indicator of ecosystem health?

Parasites are an integral and important part of all ecosystems and communities (Hudson et al. 2006), making up a substantial part of the biodiversity and biomass (Poulin & Morand 2014). With over 50% of all species on the planet being parasites or pathogens (Lafferty et al. 2008), they may directly and indirectly affect and regulate the structure of populations and communities (Dobson et al. 2008; Wood 2007). It is difficult to differentiate between less pathogenic parasites and commensalists. However, an organism is considered parasitic if it is metabolically dependent upon its host at some life stage (Noble et al. 1961).

Many parasites are species-specific or restrained to certain host taxa (Proctor & Owens 2000; Proctor 2003; Valkiūnas 2005), and this also applies to intermediate vector species (Hellgren

et al. 2008). The ability to cause or withstand harm is also species-specific for both parasite and vector, respectively (Dick & Patterson 2007; Garamszegi 2006; Palinauskas et al. 2008; Scordato & Kardish 2014), which is linked to micro-evolutionary development of immune and defensive systems (Møller et al. 2005; Møller & Rózsa 2005; Piersma 1997). This makes these dynamic systems complex and difficult to assess. Hosts and parasites may coexist in balance, co-evolved over time (Clayton et al. 1999), but can easily be disrupted by external environmental factors like introduction of alien species, alterations of habitat or other stress factors such as reduced resource availability (Daszak et al. 2000; Lafferty & Holt 2003). Maintaining defences against parasites can be costly for the host, with a trade-off of allocation of limited resources (Norris & Evans 2000; Sheldon & Verhulst 1996). In environments with high parasite pressure, hosts may allocate more to defences, thus limiting resources available for other life history components, such as fitness, reproduction and survival. It has consequently been suggested that parasites can be used as a proxy for measurement of ecosystem health (Hudson et al. 2006; Marcogliese 2005).

1.3 Avian parasites

1.3.1 An introduction to avian parasites

Most if not all birds are found to host parasites (Dabert 2005; Proctor & Owens 2000; Valkiūnas 2005), and their diverse parasitofauna is perhaps the best known for any animal group (Crompton et al. 1997). In general, the presence of parasites on wild birds have little pathogenicity (Bennett et al. 1993; Merino et al. 2000), but have been linked to reduction in fitness (Møller et al. 1997; Wood et al. 2007), long-term survival (Brown et al. 1995; Martínez-de la Puente et al. 2010; Merino & Potti 1995; Merino et al. 2000), and reproductive success (Holand et al. 2015; Kose & Møller 1999).

Bird parasites can be divided into external and internal parasites, ecto- and endoparasites. Ectoparasites are macro-parasites found on the exterior of the host, like the respiratory passages, on the skin, under the skin, on feathers and in feather quills. Endoparasites are micro-parasites found in the blood, organs and tissue of the host. Ectoparasites have a direct life cycle where all life stages can be completed upon one host, but may switch hosts during their life span, by direct transmission (Proctor & Owens 2000). Most endoparasites have a complex or indirect life cycle where sexual reproduction is completed in the primary host and a dormant or asexual reproductive stage takes place in an intermediate host (Valkiūnas 2005).

1.3.2 Definitions

As I move into the field of parasitology, a few terms need to be clarified. When investigating the effect of infestation of parasites on an individual host, the intensity (of infection) is focused upon, with intensity defined as "the number of individuals of a particular parasite species in (or on) a single infected host" (Bush et al. 1997). Infestation of parasites is also investigated with a focus on the presence or absence of parasites on individual hosts within a larger host population. Prevalence of the targeted parasites is then the preferred measurement, with prevalence defined as the proportion of infected hosts within the number of hosts examined (Bush et al. 1997).

1.3.3 Ectoparasites

The multitude of potential habitats available on each bird facilitate for multiple ectoparasite infections (Proctor & Owens 2000). The most important ectoparasite groups are chewing lice (*Ischnocera* and *Amblycera; Phthiraptera*) and feather mites (*Astigmata; Acariformes*), comprising approximately 50% and 40% of all avian ectoparasitic species, respectively (Dabert 2005). Fleas (*Ceratophyllidae; Siphonaptera*) and other mites (*Ixodida* and *Mesostigmata; Parasitiformes*) are also common. Some mites, such as ticks (Figure 1a), are free-ranging parasites that will roam the undergrowth to find a suitable host (Proctor & Owens 2000).

Feather mites (Figure 1b) consume primarily secreted uropygial gland oil from the barbules (Proctor 2003). They are so morphologically specialised that they will die within days if removed from their host and rely on physical contact with new potential hosts (Proctor & Owens 2000). Their epidemic role is controversial and much debated, as they are by many believed to have no detrimental effects on their hosts (Blanco et al. 1999; Dowling et al. 2001; Galván et al. 2012). However, a few studies have linked high feather mite loads with pox lesions (Harper 1999), poor feather quality after moult (Harper 1999), and poor body condition and loss of plumage brightness (Thompson et al. 1997).

Avian lice (Figure 1c) are the only obligate parasitic insects, feeding on feathers, scales and epidermis of the skin (Clayton & Tompkins 1995). Most species of the suborder *Ischnocera* are so specialised on feathers that their mobility are inhibited, while species of *Amblycera* are more mobile and will abandon a dead or distressed host (Johnson & Clayton 2003). Their

geographic distribution and community structure are governed by ambient humidity (Moyer et al. 2002).

Little comparative data is available on the distribution of avian ectoparasites within communities on a more regional and global scale, and even less is known about the avian ectoparasites in the tropics. One study from the Neotropics found that avian lice diversity and abundance did not differ from temperate areas (Clayton et al. 1992), while similar levels of lice intensity were found on birds in Southern China (Bush et al. 2013). Likewise, little geographic variance in feather mite loads can be found, while the species-specific variance in feather mite loads are more pronounced (Behnke et al. 1995; Blanco et al. 1997; Enout et al. 2012; Lyra-Neves et al. 2003; McClure 1989).

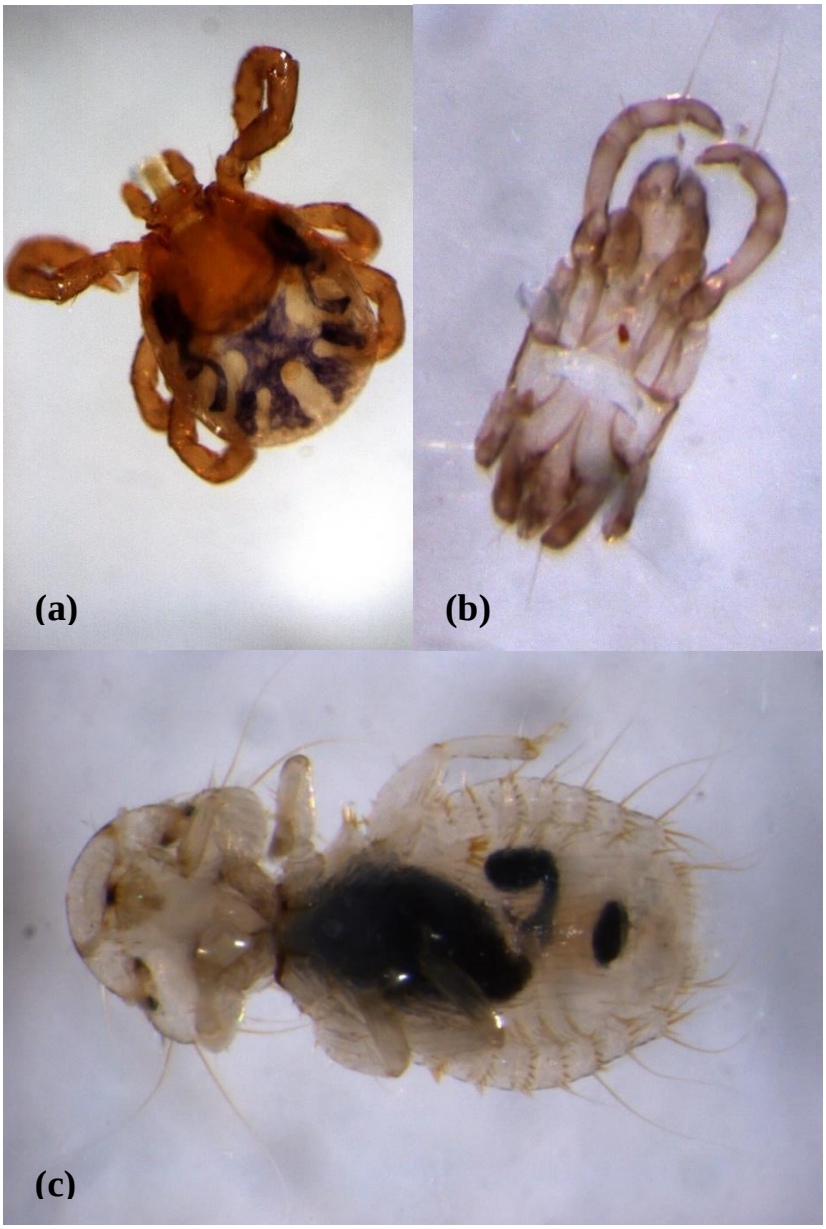

Figure 1: Photos of a (a) tick (Ixodida), (b) a feather mite (Astigmata), and (c) a chewing louse (Ischnocera). Photos: M. Fandrem

1.3.4 Blood parasites

All endoparasites found in blood films are vector-borne parasites with blood-sucking arthropods as vectors (Valkiūnas 2005), and are found in the vast majority of bird species (Atkinson & Van Riper III 1991). After an initial acute infection stage, the parasite will remain in the host in a latent chronic stage for the rest of the lifetime of the host, with sporadic relapses triggered by, for example, environmental changes or life history stages (Valkiūnas 2005). Haemosporidia, or commonly referred to as avian malaria parasites, belong to the genera *Haemoproteus* (Figure 2a+b), *Plasmodium* (Figure 2c), and *Leucocytozoon*, and invade red blood cells (RBCs). Microfilariae (Figure 2d), the first-stage larvae of filarioid nematodes (family *Onchocercidae*, superfamily *Filarioidea*), and parasitic flagellate protozoa of the genus *Trypanosoma*, can also commonly be found between the RBCs.

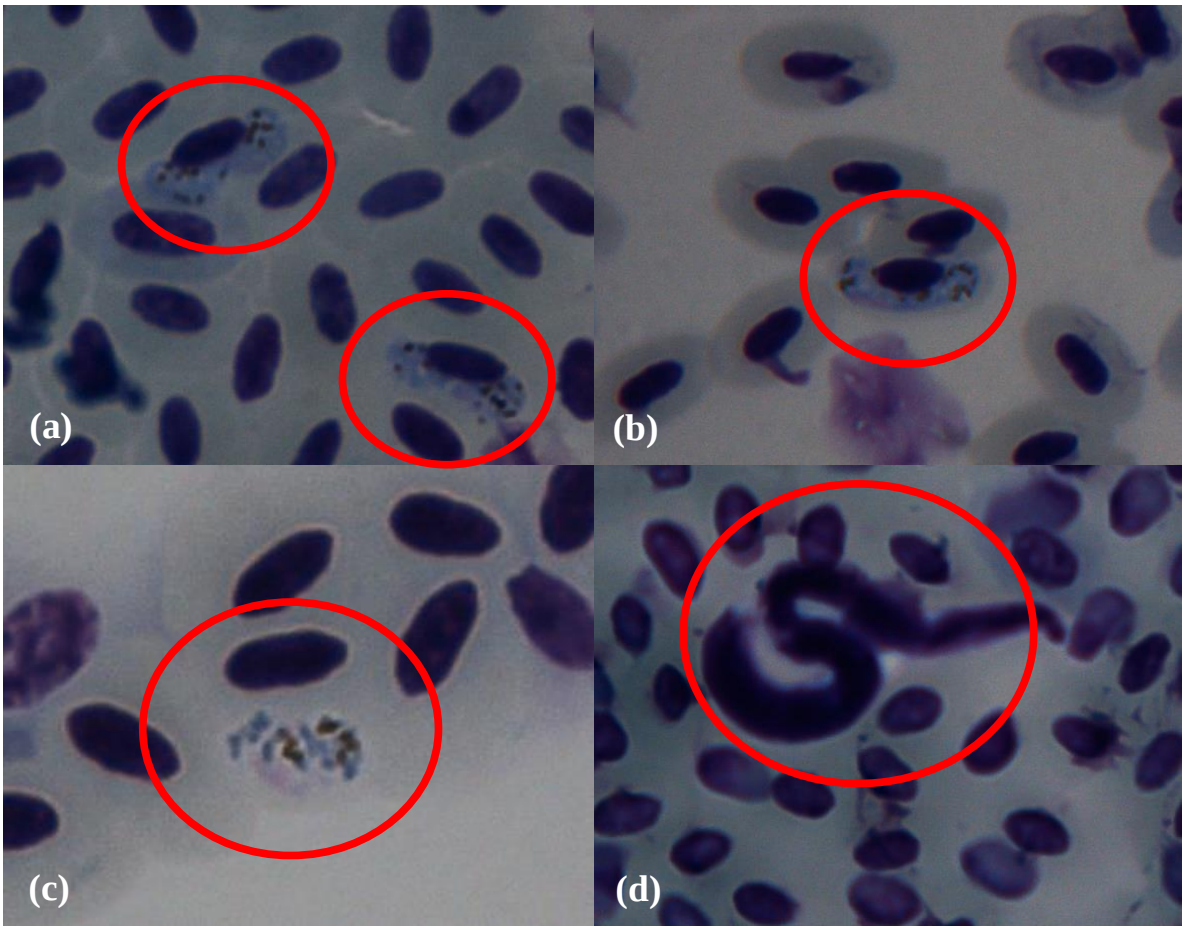

Figure 2: Examples of blood samples infected by (a) *Haemoproteus* , (b) *Haemoproteus*, (c) *Plasmodium*, and(d) filaroid microfilariae. Photos: M. Fandrem

Blood parasites are often difficult to assign to specific species, as the differences are subtle. Blood parasites are today mainly separated into various mtDNA lineages by the use of Polymerase Chain Reaction (PCR) - based detection methods (Fallon et al. 2003; Hellgren et

al. 2004; Richard et al. 2002; Valkiūnas et al. 2008). The vast majority of lineages are thought to correspond well with species, but could also reflect intra-specific polymorphism (Bensch et al. 2009). Thus, most papers discuss lineages, not species, of blood parasites, and this term will be used throughout this study.

The overall prevalence of avian blood parasites is considered regional-specific, with a tendency for higher prevalence in temperate areas compared to tropical (Greiner et al. 1975; McClure et al. 1973; Scheuerlein & Ricklefs 2004; White et al. 1978). While *Haemoproteus* clearly is the most commonly observed avian blood parasite genus worldwide, the relative frequency of the different genera may vary considerably from region to region. For example, *Leucocytozoon* is the second-most common blood parasite genus in North America with 17.7% of the birds infected (Greiner et al. 1975), while nearly absent in the Neotropics (Londono et al. 2007; Rodríguez & Matta 2001; White et al. 1978).

1.4 Forestry and avian parasites

The dynamics within the host and parasite community and the ecosystems they are found in are complex, and the possible effects of logging on the avifauna-parasite dynamics are difficult to predict. Making predictions even harder is the species-specific interactions between hosts and parasites and the intermediate vectors.

To my knowledge, only one study to date (Hill 2013) has compared parasite prevalence and infestation intensity within primary and selectively logged tropical rainforest. I will return to this study later. Logging could affect the avifauna-parasite interactions in two main ways: The effect on susceptibility by alteration of the immune responses of the hosts by increased physiological stress through habitat degradation, or by altered transmission rates and parasite population increase (Lafferty & Kuris 1999; Lafferty & Holt 2003). A change in body condition could possibly be linked to a decrease in immune responses, which will leave birds more vulnerable to infection by pathogens and parasites of both internal and external character (Norris & Evans 2000; Sheldon & Verhulst 1996). For example, malnourishment has been linked to elevated ectoparasite prevalence and intensity (Freed et al. 2008).

Transmission rates of ectoparasites and blood parasites are dependent on different processes. As ectoparasites are transmitted directly between host individuals, transmission rates are reliant

on the contact rates among host individuals. However, the effect of logging on contact rates between birds can be ambiguous. The frequency of inter- and intraspecific interactions of host individuals and subsequent transmission of ectoparasites could decrease due to a decreased abundance of host species, while interactions could also increase as suitable foraging habitats get more isolated and resources more clumped (Brearley et al. 2013; Tompkins et al. 2011). A study from Southern China found a negative correlation between avian lice prevalence and diversity and forest size, while the intensity remained the same (Bush et al. 2013). Bird abundance was correlated with forest size, indicating a density-dependent transmission rate of avian lice within the host populations (Bush et al. 2013).

As the transmission of blood parasites is highly dependent on the vector species having suitable breeding habitats, the effect of logging on prevalence relies on the ecological niche and preferences of the vector species and the specific local ecological characteristics (Yasuoka & Levins 2007). Variations in vector populations may be influenced by humidity and temperature (Gage et al. 2008; Patz et al. 2000), which have been recorded to change following logging (Brown & Whitmore 1992). Laurance et al. (2013) implied that there might be a lack of suitable breeding sites for the vector species of avian blood parasites in forest fragments and logged sites. Higher prevalence of blood parasites in continuous forest compared to forest fragments (Laurance et al. 2013), agroforest (Bonneaud et al. 2009), or deforested areas (Chasar et al. 2009) have been found. However, prevalence was not significantly different between intact cerrado, disturbed cerrado and a transition zone between rainforest and cerrado in Brazil (Belo et al. 2011).

1.5 The effects of logging on forest structure

Old selectively logged forest and primary forests are very similar in terms of structure and floristic composition (Berry et al. 2008; Brearley et al. 2004). This contrasts significantly with plantations that consist of monocultures with homogenous height and little undergrowth (Barlow et al. 2007). However, logging does affect the forest, while not having the same drastic alteration effect as land conversion. During selective logging, most of the large trees are removed, and this activity is often accompanied by structural damage to the remaining trees (Cannon et al. 1998) and soil compaction from the heavy machinery used during the timber extraction (Malmer & Grip 1990; Malmer 1996; Pinard et al. 2000). This leaves a lower, more open canopy with less structural complexity (Cleary et al. 2007; Woods 1989), a thicker

understorey (Cleary et al. 2007; Slik 2004), induced growth of pioneer species, lianas and epiphytes (Brearley et al. 2004; Heydon & Bulloh 1997), and higher gap frequency (Brown & Whitmore 1992), which increases the desiccation in the impacted and adjacent areas (Briant et al. 2010) and the effects of El Niño induced droughts (Slik 2004).

1.6 The effects of logging on Southeast Asian avifauna

Tropical forest birds are considered inherently vulnerable to habitat changes, as they tend to have small ranges and population sizes, subsequently being prone to population reductions and extirpation (Purvis et al. 2000; Sodhi et al. 2004b). Species losses within the tropical avifauna, mainly accredited to land conversion (Gaston et al. 2003), has already been recorded (Newbold et al. 2014). However, the avifauna of Southeast Asia is in general not heavily affected by selective logging, with logged forests retaining most of its species richness (Berry et al. 2010; Lambert 1992; Marsden 1998; Peh et al. 2005; Posa & Sodhi 2006), as long as the remaining forest fragments are large (Edwards et al. 2010; Lambert & Collar 2002). A high number of primary forest bird species are also retained (Edwards et al. 2011; Lambert 1992; Peh et al. 2005), although the species composition and abundance change significantly (Edwards et al. 2011; Johns 1989; Marsden 1998).

Responses to environmental and land-use changes are often related to certain functional and ecological traits of species, like feeding guild, migration pattern, social behaviour and size (Newbold et al. 2012). Previous studies have shown that species richness within feeding guilds differed little between forest type, while the abundances fluctuated (Cleary et al. 2007; Johns 1996). This can, according to Edwards et al. (2013), be explained by a clear functional overlap between species in primary forest and logged forest, where forest specialists are replaced by functionally similar secondary forest species, keeping the functional diversity nearly identical to primary forest. Overall, species that are large-bodied, forest or dietary specialists, terrestrial or canopy-dependent are the ones that are most prone to decline after logging (Lambert & Collar 2002; Meijaard et al. 2005; Newbold et al. 2014).

1.7 Why focus on avian parasites in Borneo's forests

Most of Southeast Asia is considered a biodiversity hotspot (Myers et al. 2000), due to the exceptionally high biodiversity and level of endemic species, while also having the highest

relative deforestation rate in the tropics (Sodhi et al. 2004a). Much of the loss is concentrated to insular Southeast Asia (Miettinen et al. 2011; Stibig et al. 2014) which contains about 80% of the remaining primary forest in the region (Koh et al. 2011). Borneo is the third largest island in the world and the largest land mass within insular Southeast Asia. The island is divided into the Malaysian states Sabah and Sarawak, the Indonesian provinces West-, Central-, South- and East Kalimantan, and the sultanate of Brunei.

The main threats to the forests are logging of commercially valuable timber species and land conversion to agriculture, such as palm oil and rubber plantations (Kummer & Turner 1994; Sodhi et al. 2004a). In 1960, most of the standing forest in Borneo could principally still be called primary forest. However, logging has escalated over the last 50 years or so, with repeated rounds of heavy selective logging, leaving only a few areas of pristine primary forest (Bryan et al. 2013; Gaveau et al. 2014; McMorrow & Talip 2001). Logging has for example reduced the areas of primary forest in Sabah from ~5000 km^2 in 1990 (Marsh & Greer 1992) to ~700km^2 in 2010 (Reynolds et al. 2011). The extraction rates have been among the highest globally (Edwards et al. 2011; Fisher et al. 2011a), resulting in high structural damage of the remaining forest (Cannon et al. 1994; Johns 1989; Pinard et al. 1996).

The areas under forest cover are often not just logged, but completely deforested, as the value of regenerating forests and continued forestry is competing with other commercial interests. Palm oil production alone has expanded immensely during the last decade, with an increased global production of 34.6% between 2006 and 2010 (McLaughlin 2011). This increase is mostly accredited to expansion of production in Malaysia and Indonesia, particularly in Borneo, Sumatra and peninsular Malaysia. Much of this expansion has come at the expense of peat forest and lowland dipterocarp forest (Gaveau et al. 2009; Koh & Wilcove 2009; Koh et al. 2011). In Indonesian Kalimantan, 90% of the oil palm expansion between 1990 and 2010 was initiated on former forested land (Carlson et al. 2013). Altogether, the forest cover of Borneo is estimated to have decreased from 75% in 1960 to 52.8% in 2010 (Gaveau et al. 2014). Deforestation rates are slowing, but forest cover is still declining significantly in several areas, including Sabah (Reynolds et al. 2011). Complete deforestation through land conversion is associated with high extinction rates (Brook et al. 2003; Brooks et al. 1999; Castelletta et al. 2000), and the biodiversity retained is generally low, especially in intensified monocultures (Aratrakorn et al. 2006; Danielsen et al. 2009; Donald 2004; Edwards et al. 2010).

Selective logging is the prevailing logging system, where larger trees of target species are extracted (Appanah & Turnbull 1998; Meijaard & Sheil 2007). The remaining forest, and the subsequent regrowth following logging, are acknowledged as important for carbon storage (Achard et al. 2002), but the biological conservation value is only now beginning to be recognised (Berry et al. 2010; Edwards et al. 2011; Woodcock et al. 2011). Considering that degraded logged forests have little or no legal protection and are increasingly being converted to monoculture plantations (Edwards et al. 2011), it is imperative to build on the existing knowledge base of these forests to contribute to the conservation of tropical forest biodiversity.

Several studies have focused on the impact of logging on the avifauna of Borneo, which is not surprising, considering that 358 of the 420 bird species in Borneo reside in rainforest habitats (Phillipps & Phillipps 2009)**.** These studies have looked at, for example, changes in species composition (Johns 1988; Johns 1996; Lambert 1992), functional traits (Cleary et al. 2007), and trophic flexibility (Edwards, D. P. et al. 2013). However, the avian parasites of Borneo are little explored. A search through MalAvi, an internationally recognised database for avian haemosporidian parasites (Bensch et al. 2009), shows no recorded species from the countries of Southeast Asia. Only a few studies have explicitly looked at avian parasites in Borneo (Fischthal & Kuntz 1974; McClure et al. 1973; Paperna et al. 2008), while some has been carried out in adjacent areas of Southeast Asia (e.g. Elahi et al. 2014; Ishtiaq et al. 2007).

1.8 The aim of this study

The main aim of this study was to investigate the prevalence and intensity of ectoparasites and prevalence of blood parasites in understorey birds in primary and logged forest sites in Northeast Borneo, Malaysia, and compare the results to that of Louise Hill (2013). More specifically, I aimed to evaluate the presence and distribution of avian parasites, the changes in bird-parasite dynamics after selective logging and their potential effect on the avian community. I focus here on these main questions: 1) Does parasite infestation intensity or prevalence differ in bird communities between primary and logged forest? 2) Are ecological and biological traits of the host species associated with infestation intensity or prevalence? 3) Are infestation of ectoparasites and blood parasites related? 4) Is body condition of host species correlated to parasite infestation intensity or prevalence?

2. Methods

2.1 Study site

2.1.1 Location

Fieldwork was conducted between June and October 2014 in the Yayasan Sabah Forest Management Area (YSFMA) in Sabah, North Borneo (4° 58'N, 117° 48'E). YSFMA is approximately ~10,000 km², and is one of the largest remaining continuous forest blocks in Borneo (Hazebroek et al. 2012), comprising almost one third of all forested land area in Sabah (Reynolds et al. 2011). YSFMA contains three conservation areas with preserved primary forest: Danum Valley Conservation Area (DVCA) (438km^2), Maliau Basin (588 km^2) and Imbak Canyon (300 km^2). DVCA was chosen as representative area for primary forest in this study. DVCA was gazetted as a conservation area in 1981, and encompasses the largest contiguous intact block of primary lowland rainforest remaining in Sabah (Hazebroek et al. 2012). Surrounding the DVCA is the Ulu Segama Forest Reserve (USFR) of ~2000km^2. It is considered one of the best-studied and described areas of logged rainforest in Southeast Asia (Hazebroek et al. 2012), and was therefore selected as a representative area of selectively logged forest for this study.

2.1.2 Logging history of USFR

The major form of disturbance has been selective logging, mainly of dipterocarp tree species (trees of the *Dipterocarpaceae* family) (Marsh & Greer 1992). The USFR has been logged twice. The first rotation was between 1987 and 1991, and the second between 2000 and 2007 (Fisher et al. 2011b), giving it a very short regeneration period. During the first rotation dipterocarp trees with diameter at breast height (DBH) > 60 cm was targeted and the yield was about 120 m^3ha^{-1} (sometimes as high as 170 m^3ha^{-1}), which is among the highest recorded in any tropical country (Marsh & Greer 1992). During the second rotation, the minimum DBH was decreased to >40 cm, more species were approved for harvest, and new areas previously considered too steep were cut (Edwards et al. 2011). However, yield was still very low compared to the first rotation, averaging around 35 m^3 ha^{-1}. After two logging rotations, the forest was left in a highly degraded condition, but due to its continued value for biodiversity (Berry et al. 2010; Edwards et al. 2011; Johns 1996), the entire USFR has been set aside in perpetuity for protection of natural forest cover and sustainable management (Reynolds et al. 2011).

2.1.3 Climatic conditions

The DVCA and USFR have an undulating topography, lying generally between 100 and 400 m.a.s.l.. A typical perhumid equatorial climate with little annual seasonality prevails, with only slight climatic changes caused by monsoonal alterations of wind direction. Severe droughts linked to El Niño events occasionally occur (Walsh & Newbery 1999). The average annual rainfall is 2850 mm, making the area intermediate in wetness compared to the drier east coast and the wetter regions of southwestern and central Borneo (Walsh & Newbery 1999). The relative humidity within the understorey of the closed forest is generally above 90%, with daily temperature ranging between 21 ℃ and 28.5 ℃ (Brown & Whitmore 1992).

2.1.4 Ecological description of study area

The area comprises primarily lowland forest dominated by dipterocarp trees in the upper and lower canopy. The dipterocarps contribute 60-80% of the total volume of large trees (Marsh & Greer 1992; Newbery et al. 1992), with other important tree families encompassing Lauraceae, Meliaceae, Euphorbiaceae, and Myrtaceae (Cleary et al. 2007; Newbery et al. 1992). The trees form a dense canopy of between 35-45 m in height, with emergent trees reaching up to 60-70 m (Campbell & Newbery 1993). Trees make up the prevailing life form in these types of habitats, with approximately 130 tree species/ha recorded in DVCA (Newbery et al. 1992), providing habitat for 317 species of birds (Hazebroek et al. 2012).

2.2 Fieldwork

2.2.1 Mist netting

Birds were sampled with mist nets along linear transects. Fifteen nets (12 × 2.7 m) were erected end-to-end on two transects (separated by >250 metres) at each site in primary (N=3) and logged forest (N=3). The six sites were randomly selected on an east-west direction, covering a landscape of approximately 115 km across (Figure 3). Each site was separated by a minimum of 2 km. Nets were opened for two consecutive days from 6.00 am to 12.00 am at each site, and nets were checked every hour. All sites were visited three times. Nets were closed during rainfalls, and the closure time was added to same day or next visit to same site. All birds captured were banded, measured, sampled for parasites and then released. Recaptures previously sampled for parasites were not considered, as they may not have re-established their

ectoparasite load. Cloth bags, used to transport birds from net to banding site, were used only once per day if possible, inverted if used twice, and washed after use, to prevent cross-contamination of ectoparasites.

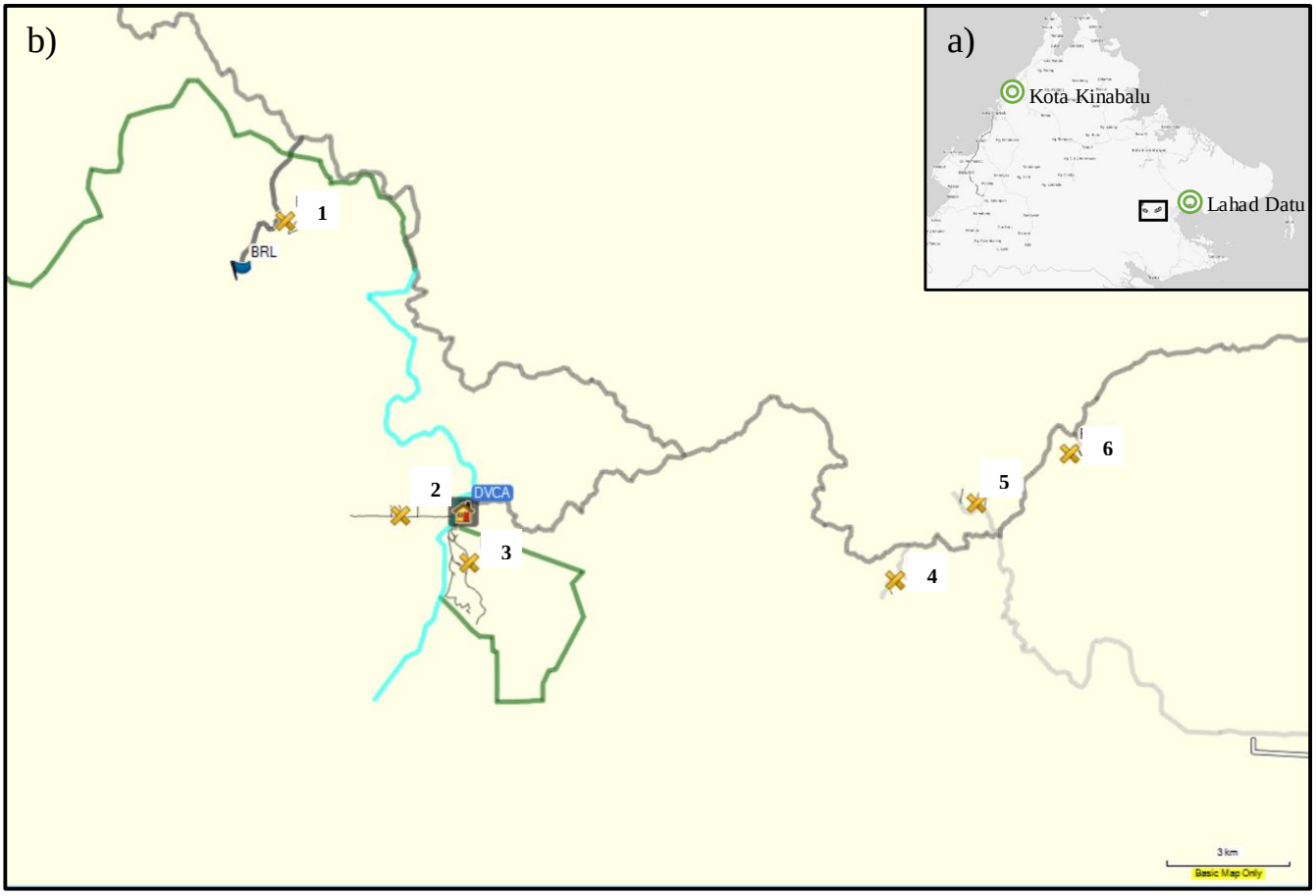

Figure 3: a) Map of Sabah, Malaysian Borneo. The rectangular box represents the study area. b) Map of research area within the YSFMA. Numbers represents sites (1,2,3 in primary forest, 4,5,6 in logged forest). Blue line specifies the Segama River. Green lines represent the borders of the DVCA (Danum Valley Conservation Area; primary forest). Areas west of the Segama river also belong to the DVCA. Roads are indicated with grey lines: the dark grey lines being main roads, while paler grey are old logging roads and trails. Blue flag shows the location of the resort BRL (Borneo Rainforest Lodge) and the house show the location of the field centre for DVCA.

2.2.2 Species identification and assessment of functional and ecological traits

Birds were identified to species level in field using field guides (Myers 2009; Phillipps & Phillipps 2009) and controlled by field experts (Dr David Edwards and Dr Suzanne Tomassi). For practical implementations, all species were given an abbreviation derived on their common name (Table 1).

2.2.3 Ecological and functional traits of birds

A number of functional and ecological traits considered of relevance was noted for the encountered species (Table 1). Traits of each species were based on Handbook of the Birds of the World Alive (HBW; del Hoyo 2014), Lambert (1992), Edwards et al. (2011), and Cleary et al. (2007). All functional traits were recorded as categorical variables.

Birds were assigned to the feeding guilds frugivores (F), insectivores (I), nectarivores (N), carnivores (C), or combinations of these (e.g. F,I). Foraging strategy was recorded as "foliage gleaning", "flowerpecking", "sallying", or "undergrowth". Species associated with terrestrial feeding, undergrowth and low understorey movements, were pooled as "undergrowth", as birds categorised as "terrestrial" and "low understorey" were assembled of too few species. Conservation status was defined as threatened (T) (including the red list categories "near-threatened", "vulnerable", "endangered" and "critically endangered"), or of least concern (LC) (species defined as the red list category "of least concern") (IUCN 2014). Distribution was categorised as endemic or non-endemic to the defined Sundaland area. Body size was recorded from HBW as the mean of the estimated body size range of the species, and pooled into the size-groups I, II, III, and IV, representative of a body size 10-12 cm, 13-15 cm, 16-18 cm, and 19 cm and above, respectively. In addition, primary forest dependence was assessed from calculated change in abundance from primary to logged ($N_{logged}/N_{primary}$) for each species, using all of the 2014 captures (N=1461). Species with a decline in abundance in logged forest (0.0-0.75) was grouped as primary forest specialists. Species with no or small changes in abundance from primary to logged (0.75-1.50) was grouped as generalists, while species with a clear increase in abundance in logged forest (>1.50) was grouped as logged forest specialists.

Table 1: Compilation of species information with common name, species abbreviation, scientific name, family, and functional traits specifications.

Species abbreviation	*Common name*	*Latin name*	*Family*	*Feeding guild*	*Conservation status*	*Foraging strategy*	*Body size (cm)*	*Body size (group)*	*Distribution*	*Abundance change*	*Forest dependence*
BCBAB	Black-capped Babbler	*Pellorneum capistratum*	Timaliidae	I	LC	Undergrowth	17	III	Endemic	1.00	Equal
BFUL	Brown Fulvetta	*Alcippe brunneicauda*	Timaliidae	F,I	T	Foliage gleaning	14	II	Endemic	2.44	Secondary
BHBUL	Black-headed Bulbul	*Pycnonotus atriceps*	Pycnonotidae	F,I	LC	Foliage gleaning	17	III	Non-endemic	25.00	Secondary
CRBAB	Chestnut-rumped Babbler	*Stachyris maculata*	Timaliidae	I	T	Undergrowth	17	III	Endemic	3.25	Secondary
CWBAB	Chestnut-winged Babbler	*Stachyris erythroptera*	Timaliidae	I	LC	Undergrowth	12	I	Endemic	2.58	Secondary
FBAB	Ferruginous Babbler	*Trichastoma bicolor*	Timaliidae	I	LC	Undergrowth	17	III	Endemic	1.29	Equal
FBTBAB	Fluffy-backed Tit-Babbler	*Macronus ptilosus*	Timaliidae	I	T	Undergrowth	15	II	Endemic	3.00	Secondary
GCBUL	Grey-cheeked Bulbul	*Alophoixus bres*	Pycnonotidae	F,I	LC	Foliage gleaning	22	IV	Endemic	1.08	Equal
GHBAB	Grey-headed Babbler	*Stachyris poliocephala*	Timaliidae	I	LC	Undergrowth	15	II	Endemic	2.09	Secondary
HBAB	Horsfield's Babbler	*Malacocincla sepiaria*	Timaliidae	I	LC	Undergrowth	14	II	Endemic	1.17	Equal
HBBUL	Hairy-backed Bulbul	*Tricholestes criniger*	Pycnonotidae	F,I	LC	Foliage gleaning	16	III	Endemic	1.70	Secondary
LBBFLY	Large-billed Blue Flycatcher	*Cyornis caerulatus*	Muscicapidae	I	VU	Sallying	14	II	Endemic	0.33	Primary
LSPHUN	Little Spiderhunter	*Arachnothera longirostra*	Nectariniidae	N,I	LC	Flowerpecking	15	II	Non-endemic	2.76	Secondary
MBAB	Moustached Babbler	*Malacopteron magnirostre*	Timaliidae	I	LC	Foliage gleaning	16	III	Endemic	0.63	Primary
ODKING	Oriental Dwarf Kingfisher	*Ceyx rufidorsa motleyi*	Alcedinidae	I	LC	Undergrowth	14	II	Endemic	1.40	Equal
PBBUL	Puffy-backed Bulbul	*Pycnonotus eutilotus*	Pycnonotidae	F,I	T	Foliage gleaning	18	IV	Endemic	6.50	Secondary
PNSUN	Purple-naped Sunbird	*Hypogramma hypogrammicum*	Nectariniidae	N;I	LC	Flowerpecking	15	II	Non-endemic	1.05	Equal

Table 1 continued.

Species abbreviation	*Common name*	*Latin name*	*Family*	*Feeding guild*	*Conservation status*	*Foraging strategy*	*Body size (cm)*	*Body size (group)*	*Distribution*	*Abundance change*	*Forest dependence*
PSUN	Plain Sunbird	*Anthreptes simplex*	Nectariniidae	N,I	LC	Flowerpecking	12	I	Endemic	3.60	Secondary
RCBAB	Rufous-crowned Babbler	*Malacopteron magnum*	Timaliidae	I	NT	Foliage gleaning	17	III	Endemic	0.44	Primary
REBUL	Red-eyed Bulbul	*Pycnonotus brunneus*	Pycnonotidae	F,I	LC	Foliage gleaning	17	III	Endemic	3.00	Secondary
RPIC	Rufous Piculet	*Sasia abnormis*	Picidae	I	LC	Foliage gleaning	10	I	Non-endemic	2.53	Secondary
RWPHIL	Rufous-winged Philentoma	*Philentoma pyrhoptera*	Monarchidae	I	LC	Sallying	16	III	Endemic	1.30	Equal
SBUL	Spectacled Bulbul	*Pycnonotus erythropthalmos*	Pycnonotidae	F,I	LC	Foliage gleaning	18	IV	Endemic	2.50	Secondary
SCRBAB	Scaly-crowned Babbler	*Malacopteron cinereum*	Timaliidae	I	LC	Foliage gleaning	15	II	Non-endemic	0.47	Primary
STBAB	Short-tailed Babbler	*Malacocincla malaccensis*	Timaliidae	I	T	Undergrowth	14	II	Endemic	1.46	Equal
WCFORK	White-crowned Forktail	*Enicurus leschenaulti*	Turnidae	I	LC	Undergrowth	15	IV	Non-endemic	1.60	Secondary
WCSHAM	White-crowned Shama	*Copsychus stricklandi*	Turnidae	F,I	LC	Undergrowth	25	IV	Non-endemic	1.86	Secondary
YBBUL	Yellow-bellied Bulbul	*Alophoixus phaeocephalus*	Pycnonotidae	F,I	LC	Foliage gleaning	27	IV	Endemic	0.92	Equal
YBFLPEC	Yellow breasted Flowerpecker	*Prionochilus maculatus*	Dicaeidae	N,I	LC	Flowerpecking	10	I	Endemic	0.73	Primary

2.2.4 Measurements of body condition

The length of the left wing from the bend of the elbow and down to the maximum chord was measured with a wing ruler to the nearest mm, as described in The North American Banders' Study Guide (The North American Banding Council 2001). Fat and muscle score were recorded according to the guidelines of the British Trust for Ornithology (BTO), with visual inspection of tracheal pit and pectoral muscles, as described by Gosler (1991) and Harper (1999). Fat in the tracheal pit and abdominal region was scored on a six-point scale (0-5) according to colour and fullness of fat deposits, where a '0' indicates no visible fat and '5' indicates that the tracheal pit is filled with fat storage of a cream white colour. The pectoral muscles was scored according to their shape on a four-point scale (0-3): '0' indicates a bird in poor condition where the muscle is concave with the sternal keel prominent, and a bird scoring '3' indicates a bird in excellent condition where the muscle is convex and hiding the keel.

2.2.5 Dust-ruffling

I used dust-ruffling, a common, non-intrusive method, to collect ectoparasites, as described by Clayton and Walther (1997). An insecticide powder is applied to the feathers of the bird whereupon the paralysed ectoparasites will loosen their grip and fall off onto a clean collection surface placed underneath the bird when the feathers are ruffled.

A commercial insecticide containing the natural ingredient pyrethrin with the synergist piperonyl butoxide (Aristopet Flea and Tick Powder; Beaphar Pharmaceuticals and Masterpet Corporation Ltd.), containing 0.15% pyrethrin and 1.0% piperonyl butoxide, was used. These chemicals are considered to have no negative side effects on the bird (Clayton & Tompkins 1995) and are biodegradable with little or no environmental effect (Casida 1980). Pyrethrin is derived from pyrethrum, which is extracted from the flowers of chrysanthemums (Walther & Clayton 1997). It is fast acting; killing or immobilising the ectoparasites and other small invertebrates immediately.

The dust powder was worked into the feathers and feather tracts of the wings, body, tail, top of legs and neck with a soft paintbrush, until all areas were lightly covered in dust, while holding the bird over a white sheet of paper inside a plastic folder. The head and face was avoided, as the powder can be somewhat irritating to the eyes. The feathers were then gently ruffled for 3 minutes by using the fingers of one hand while holding the bird in a handlers grip with the

other, making sure that the bird's wings were restrained as any flapping of wings could potentially disperse any ectoparasites off the collection surface. As the parasites are small and almost impossible to see with the naked eye, I chose to ruffle each bird for 3 minutes, instead of repeated sessions of ruffling until all visible parasites were removed. Three minutes was considered appropriate for the body size of a species like Common Starling (*Sturnus vulgaris*) (Koop & Clayton 2013), which is approximately the same size as the largest birds in this study. All particles falling from the bird onto the white collection surface were then collected into a 5 ml vial with a screw cap containing 95% ethanol. The see-through plastic folder made it easy to detect all darker particles fallen onto the white surface while not getting the paper smudged and wet. It also simplified the collection and cleaning, as the surface of the plastic folder was smoother than the paper. The paintbrush and the collection surface were thoroughly cleaned between samples, to avoid erroneous host-parasite records.

2.2.6 Blood sampling

Blood was obtained from a toenail clip. The tip of a claw was clipped with a pair of nail clippers after being cleaned with alcohol. Subsequently, a drop of blood was extracted onto the end of a standard clean microscope slide with a frosted end. Another slide was used as a spreader, held in a slight angle of about 45 degrees, and pushed smoothly across the slide using the push-slide technique to achieve a single-cell-layer (Campbell & Ellis 2013). After clipping, a cotton ball was held firmly against the cut. The bleeding was stopped by applying a haemostatic agent, either corn flour or styptic powder, when not seizing on its own. To reduce stress for the bird and to avoid getting the dust ruffling powder into the cut, the collection of blood samples was performed last and as quickly as possible before releasing the bird.

After preparing the smear, the samples were left to air-dry before submersion in 100% methanol for 30 seconds (Owen 2011). The completed slides were placed vertically to drain the alcohol before being placed horizontally in a box with clean tissue paper between each slide. The slide used as a spreader was cleaned thoroughly, to avoid any contamination between samples. The slides were transferred to a slide box containing silica gel in the afternoon for complete drying.

2.3 Laboratory analysis

2.3.1 Ectoparasite identification

The contents of the ectoparasites vials were flushed into a petri dish and examined with a dissecting microscope with 11.5× magnification. The contents were first examined on a white background, then on a black background, controlling for small, almost see-through organisms that could have been overlooked on the white background. Ectoparasites were sorted into groups of feather mites (*Astigmata),* other mites (*Ixodida, Mesostigmata*), lice (*Phthiraptera*), winged insects (*Diptera, Hymenoptera, Thysanoptera*) and others (*Coleoptera, Collembola, Aranea*) by visual inspection using Knee and Proctor (2006) and Rothschild and Clay (1957), in addition to various online sources. All individuals were counted, photographed (Figure 1), using a Leica DFC320 camera attached to the dissection microscope, and then moved to a new vial containing 70% ethanol using a 3 ml pipette or a pair of tweezers. The remaining debris was returned to the original vial for possible later examination. Only the lice, feather mites and other mites were included in the analysis, as most other groups could be excluded as erroneous catches.

2.3.2 Blood parasite identification

The blood smears were stained with a standard stock solution of Giemsa's stain (Improved R66 solution Gurr), based on methylene blue and eosin. The working solution was prepared on the same day as staining, with 10 mL of standard stock solution in 100 mL phosphate buffered water with pH 7.2. The slides were first fixed in methanol for 3 minutes before being submerged vertically in the staining solution for 45 minutes. The slides were then rinsed with tap water, until little or no colouration remained. The slides were kept in drying racks in a vertical position overnight to drain and dry, and were later stored in slide boxes with silica gel.

The red blood cells (RBCs) in the cellular monolayer was examined with an oil-immersion microscope. First under 100× magnification, to spot larger parasites like *Leucocytozoon* and microfilariae larvae of filaroid nematodes. Four areas with qualified monolayered RBCs were then choosen. The four areas were chosen in different sections of the smear, as infections may exhibit clumping and not be evenly distributed (Godfrey Jr et al. 1987). These were subsequent examined using 1000× and 400× field of magnification for smaller intracellular parasites like *Plasmodium* and *Haemoproteus*. For the use of the 1000× lens, immersion oil was placed

directly onto the smear and the lens lowered into the oil for scanning. Nine fields of view in each of the four areas were examined, in all 36 fields of view at 1000× field of magnification. The majority of chosen areas were started along the edges of the smear and continued towards the centre, as larger blood parasites like *Leucocytozoon* and *Trypanosoma* tend to concentrate along the tail and edges of the smear, and parasitized RBCs in heavier infections are known to be concentrated here (Godfrey Jr et al. 1987). If not found to be infected after this, more fields of view at both 1000× and 400× were examined to conclude whether or not the blood smear was 'below detectable limits' (BDL) of an infection. Negative samples do not necessarily mean that the individual is not infected, only that the infection was not discovered at the measures taken or not present in the specific blood sample taken from the individual. A field of view at 1000× with high density of RBCs contained approximately 350 RBCs and was considered 'saturated'. Fields of view considered 'unsaturated' was complemented by adding additional fields. Approximately 20,000 RBCs were examined in total per slide. This is approaching the amount of 25,000 RBCs recommended by Valkiūnas (2005), to be able to detect low-level chronic infections and adequately determine the prevalence of blood parasites, which few studies have exceeded (Garamszegi 2010). Reference pictures were taken of some fields of view on each slide as well as of all suspicious cells (Figure 2).

The infected smears was grouped into *Haemoproteus, Leucocytozoon, Plasmodium,* and microfilariae. The intracellular infections were recorded as *Haemoproteus* if the halter-shaped mature gametocyte was observed, while infections with larger, roundish gametocytes and displacement of the cell nucleus were recorded as *Plasmodium,* after Valkiūnas (2005). To avoid false positives, only smears with cells clearly infected with mature gametocytes or displaying >3 appearances of immature gametocytes were included as infected in the current study. Infections of uncertain genera were photographed and emailed to Dr Robert Adlard at the Queensland Museum (Australia) for additional inspection. After examination, the slides were cleansed with xylene to remove the immersion oil before being returned to the slide boxes with silica gel.

2.4 Dataset compilation

A total of 395 individuals of 34 species were sampled in 2014: 207 with dust ruffling, 391 with blood sampling, and 199 individuals with both methods.

2.4.1 Ectoparasite dataset

All 207 dust ruffling samples from 2014 were examined (N=106 and N=101 in primary forest and logged forest, respectively). For the analysis of ectoparasites, the 2014 data was combined with data from 2013, collected with identical methods from primary (N=98) and logged (N=100) forest in and around Maliau Basin Conservation Area (4°44'N, 116°58'E), YSFMA, courtesy of Louise Hill (2013). In total, 382 individuals from 24 species were analysed with respect to ectoparasites (N=188 and N=194, primary and logged forest, respectively). Ten species were excluded due to missing samples from one forest type.

2.4.2 Blood parasite dataset

Of the 391 blood smears, 258 were screened for the presence of avian blood parasites (N=128 and N=130 in primary and logged forest, respectively), from 18 species and 7 families. The twelve species with highest sample sizes in both forest types were examined for blood parasites, supplied with six species with high amounts of corresponding dust ruffling samples and samples from both forest types. Samples from 2013 were not included in the final analysis due to different methodological approaches.

2.4.3 Combined datasets

Of the 199 double-tested individuals for both ectoparasites and blood parasites, 165 of the blood smears were screened and analysed for correlation between infection of blood parasites and ectoparasites. When testing for correlations in body condition measurements and forest types, all samples included in the datasets for ectoparasites and blood parasites were used, with duplicates removed (N=468).

2.5 Statistical analysis

All statistical models were run in RStudio version 0.98.1102 (© 2009-2014 RStudio, Inc.), with R version 3.2.0 (R Core Team 2015), and figures were created in Veusz version 1.22 (© 2003-

2014 Jeremy Sanders and contributors). All means are given with ± 1 SE in text, figures and tables, unless stated otherwise.

I used generalized linear-mixed models (GLMMs) (the *glmer.nb* and *glmer*-functions from the *lme4*-package; Bates et al. 2014) to test for any differences in intensity or prevalence of ectoparasites and blood parasites between the various explanatary variables. The distribution of ectoparasites on their host population is usually highly aggregated with many hosts having low numbers of ectoparasites and a few individuals having very high numbers, causing overdispersion (Clayton & Walther 1997; Shaw & Dobson 1995). Another source of overdispersion is the variability in detection efficiency, as the methods will not record 100% of present ectoparasites. Overdispersion is not easily corrected for with only a transformation of the data, especially when the mean is low (O'Hara & Kotze 2010). All tests with the ectoparasites as response variable were thus run with with a negative binomial error structure and log link function that includes an overdispersion parameter (theta) giving invididual-level variability, which is empirically shown to be the best solution for overdispersed count data (Ismail & Jemain 2007; Shaw & Dobson 1995). The aggregated distributions of ectoparasites (and also blood parasites) prohibited the use of full global models with all the explanatory variables included. Subsequently, separate models were used. This may be overcome with larger sample sizes.

To test for differences of intensity of ectoparasites between forest types, one model was set in the form of: *"Intensity~ forest type + random variables".*
The other explanatory groups were tested singularly, set in the form of:
*"Intensity~ explanatory group * forest type + random variables".*

The models were optimised by dropping the interaction term and the forest type variable, when these showed as non-significant in ANOVA Chi-square deletion tests. The levels of the various groups were then contrasted against each other by altering the default reference level and rerunning the tests. The difference in intensity between forest types within each level of the explanatory group was then tested by subsetting the dataset to only include the target level, or if the interaction term was kept, by altering the reference level and assess the main effect over forest type. Body size was set as an ordered factor and tested for any trends between parasitic intensity and increasing body size.

The models of ectoparasites were validated through plotting residuals *vs*. fitted residuals and assessing the possible overdispersion quantitatively with the function *overdisp_fun* in *glmm_fun*.R, provided by Bolker et al. (2011), calculating the Chi-square distribution of the sum of squared Pearson residuals.

Differences in prevalence of infection of blood parasites were tested similarily, but with logistic GLMMs with binomial error structure and logit link function, and with prevalence as response variable. The models of blood parasites were validated by assessing binned plots of residuals *vs*. fitted values with the *binnedplot*-function (from the *arm*-package; Gelman & Su 2015). Overdispersion cannot be modelled for binary data with a Bernoulli distribution (Molenberghs et al. 2012; Skrondal & Rabe-Hesketh 2007).

Indicators and measurements for body condition (fat score, muscle score and individual wing length) were tested against both ectoparasites and blood parasites, separately. Fat score and muscle score were set as ordered factors, testing for a linear or non-linear trend in parasitic prevalence and intensity, in the same way as wing length. The models were set in the form of: *"Intensity/Prevalence~ body condition * forest type + random variables".*

Due to the nested design of the study, transects nested within sites (1|Site/Transect) was included as random variables in all models to account for variation or lack of independence within forest types. Differences between the sites used in 2013 and 2014 for sampling ectoparasites would mostly be accounted for through this. However, in several models transects and plots explained little or nothing of the variation in the residuals. Adding year as random factor was tested and this did not alter the results, or account for more of the residual variance. In addition, species nested within taxonomic families (1|Family/Species) was included as random factors, to account for species-specific or phylogenetic differences, in the models for forest type and body condition measurements.

Low sample sizes and skewedness in the dataset created large variances and made convergence of models difficult. To increase the chance of models converging (i.e. the algorithm converging toward an optimal solution), all models were run with the additional function

"glmerControl(optimizer="bobyqa", optCtrl=list(maxfun=100000))", for an alternative optimizer and an increase in maximum number of iterations (Bates, et al. 2014).

The relationship between prevalence of blood parasites and intensity of ectoparasites were tested using the combined dataset, with all double-tested individuals of 2014, with a negative binomial GLMM set in the form of:
"EPtot~ BPtot + random variables".

Due to lack of normality, the differences in the distributions of wing length measurements, fat scores and muscle scores between forest types were all tested with Kruskall-Wallis rank sum tests, while Kendall tau rank sum tests were used to look for any correlations between fat score, muscle score and wing length.

2.6 Mantel tests

Census points separated by more than 200 m in tropical rainforest habitat have been shown to be statistically independent of each other (Hill & Hamer 2004). This study should then be well clear of any spatial autocorrelation of measurements. The possible spatial autocorrelation in intensity of ectoparasites and prevalence of blood parasites within plots and transect were still tested through Mantel tests, testing the congruence between two distance matrices. No spatial autocorrelation was found between intensity of ectoparasites and transects (r=-0.025, p=0.538), or between prevalence of blood parasites and transects (r=0.007, p=0.377).

3. Results

3.1 Ectoparasites

3.1.1 Distribution of ectoparasites

Approximately 75% of the dust-ruffled birds had one or more ectoparasites (Table 2a), with 69.6% being infected by feather mites (Table 2b). The parasite intensity had a typically aggregated distribution, with more than half (55.0%) of the birds having low infestations of 1 to 10 ectoparasites registered, and only 2.6% having more than 50 ectoparasites (Table 2a). A total load of 154 ectoparasites was the highest number recorded on any individual. Feather mites was the main group of ectoparasites registered, and only small numbers of lice and other mites were recorded (Figure 4). Of the infested birds, 20.9% had multiple infestations of more than one parasite group. Only 1.6% of the infested individuals had all three parasitic groups present. The overall mean ectoparasite load was 8.4 ± 0.88 (SE) per bird, with a median of 2.

Table 2: (a) The distribution of ectoparasites within the avian community, and (b) the overall percentage of infected birds with either of the ectoparasite groups or with multiple infections. Abbreviations: FM= Feather mites, M= other mites, L= lice.

(a)

Number of ectoparasites	*Number of birds*	*Percentage*
0	94	24.6%
1-10	210	55.0%
11-20	34	8.9%
21-50	34	8.9%
51-100	7	1.8%
>100	3	0.8%
Total infested	288	75.4%

(b)

Ectoparasite groups	*Number of birds*	*Percentage*
FM	266	69.6%
M	70	18.3%
L	38	10.0%
>1 type	80	20.9%
FM:M:L	6	1.6%

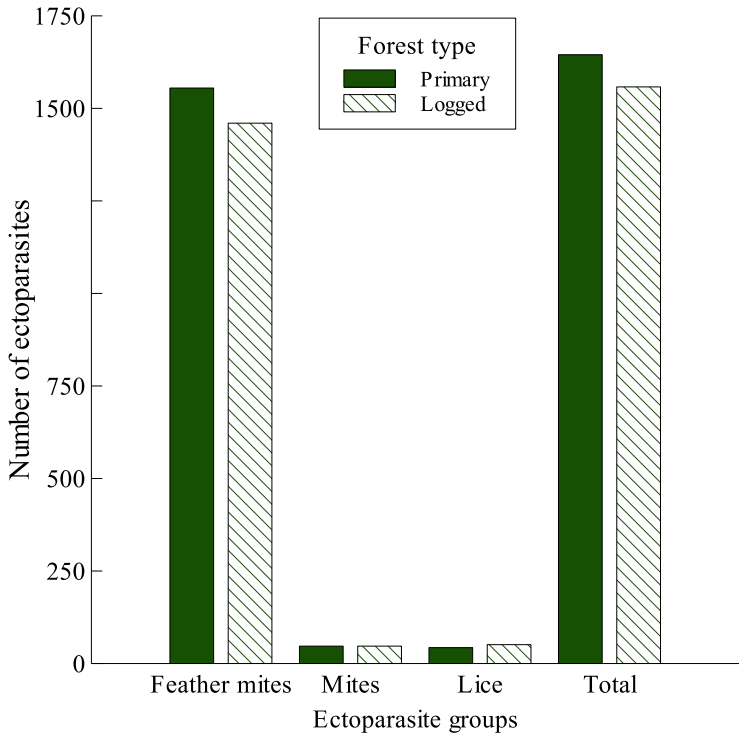

Figure 4: Total number of ectoparasites extracted with dust-ruffling for each ectoparasite group in primary and logged forest.

3.1.2 Differences between primary and logged forest

In total, 1645 and 1558 ectoparasites were recorded in primary and logged forest, respectively. Using the dataset from 2013 and 2014 pooled (excluding species captured only in one forest type), there was no significant difference in the mean intensity of ectoparasites per bird between unlogged (8.75 ± 1.21; N=188) and logged (8.03 ± 1.27; N=194) forest (GLMM; t=-0.98, p=0.33). The prevalence of ectoparasites did not differ between forest types either (GLMM; z=-1.13, p=0.26), with 78.7% (0.79 ± 0.03) of birds being infected in primary forest compared to 72.2% (0.72 ± 0.03) in logged forest.

When analysed separately, the datasets from 2013 and 2014 were markedly different. The mean infestation intensity of ectoparasites per bird in primary forest was more than twice as high as the mean in logged forest in the 2013 dataset (8.25 ± 2.29 and 4.20 ± 0.75), while the mean infestation intensity was slightly higher in logged forest compared to primary in the 2014 dataset (9.40 ± 2.51 and 12.56 ± 1.60 in primary and logged forest, respectively; GLMM; t=0.03, p=0.97).

3.1.3 Differences between species and families

The investigation of differences between species was restricted to 11 species with a total sample size of ≥10 with ≥5 samples from each forest type. The mean intensity of ectoparasites across species differed significantly (ANOVA on GLMM; $F_{10,271}$=11.34, P<0.0001; Figure 5a), and the species-specific infestations varied from *Hypogramma hypogrammicum* (PNSUN) having lowest recorded mean intensity of ectoparasites (1.00 ± 0.24) to *Tricholestes criniger* (HBBUL) having the highest (21.60 ± 3.99). None of the species exhibited any significant differences in mean infestation intensity between primary and logged forest (Table 3 & Figure 5b), and there was no interaction between forest types and species (ANOVA Chi-square deletion test on GLMM; Chi-square=16.68, df=11, p=0.12).

Following the same procedure, five bird families with sample sizes ≥10 and ≥5 in each forest type were compared. The families differed significantly in mean infestation intensity of ectoparasites (Figure 5c) with *Dicaeidae* having the lowest (1.36 ± 0.36) and *Pycnonotidae* having the highest (14.54 ± 2.42). Only *Nectariniidae* differed between forest types, with lower mean infestation intensity of ectoparasites in logged forest compared to primary (Table 3 & Figure 5d). No interaction between forest type and families were found (ANOVA Chi-square deletion test on GLMM; Chi-square=5.50, df=5, p=0.36).

Prevalence for both species and families followed a similar pattern as intensity, with the species and families having highest mean intensity of ectoparasites also having the highest prevalence (Table 4 & Table 5). All species were infected with ectoparasites, with a prevalence ranging from a proportion of 0.46 to 1.00, and the relative prevalence among families ranged from 0.54 to 0.98.

Table 3: Results of the GLMM models on differences in mean intensity of avian ectoparasites between forest types (primary and logged) in the subset of species and families with sample size ≥10 and ≥5 in each forest type. Intercepts, estimates and SE are given in log-transformed numbers. Significant p-values are marked in bold (p<0.05 significance level).

	residual df	***Intercept***	***Estimate***	***SE***	***t-value***	***p-value***
Species						
Tricholestes criniger (HBBUL)	20	2.85	0.10	0.50	0.20	0.84
Trichastoma bicolor (FBAB)	22	2.56	0.04	0.68	0.06	0.96
Stachyris erythroptera (CWBAB)	22	0.90	1.09	0.59	1.84	0.07
Malacocincla malaccensis (STBAB)	18	0.12	-0.13	0.68	-0.19	0.85
Malacocincla sepiaria (HBAB)	11	2.09	-0.43	0.80	-0.54	0.59
Sasia abnormis (RPIC)	13	1.74	-0.51	0.57	-0.90	0.37
Alophoixus phaeocephalus (YBBUL)	10	1.36	0.28	0.69	0.40	0.69
Arachnothera longirostra (LSPHUN)	61	0.09	-0.09	0.32	-0.27	0.79
Alcippe brunneicauda (BFUL)	8	1.42	-1.02	1.09	-0.93	0.35
Prionochilus maculatus (YBFLPEC)	23	0.34	-0.57	0.62	-0.91	0.37
Hypogramma hypogrammicum (PNSUN)	22	0.27	-0.88	0.52	-1.70	0.09
Families						
Pycnonotidae	45	2.31	0.50	0.40	1.25	0.21
Timaliidae	158	1.98	0.07	0.40	0.17	0.87
Picidae	13	1.74	-0.51	0.57	-0.90	0.37
Nectariniidae	88	1.38	-0.67	0.31	-2.16	**0.03**
Dicaeidae	23	0.34	-0.57	0.62	-0.91	0.37

Table 4: Mean intensity of ectoparasite infestation and the prevalence of ectoparasites among all sampled avian species; indicating the number of bird captures per species (No.), mean ectoparasite load (Mean), standard error (SE), and prevalence (Prev.) in each forest type and overall.

	Primary forest					***Logged forest***					***Overall***				
Species	**No.**	**Mean**	**SE**	**Prev.**	**SE**	**No.**	**Mean**	**SE**	**Prev.**	**SE**	**No.**	**Mean**	**SE**	**Prev.**	**SE**
Pellorneum capistratum (BCBAB)	3	6.0	4.58	0.67	0.33	2	22.0	9.00	1	0	5	12.4	5.46	0.80	0.20
Alcippe brunneicauda (BFUL)	7	4.1	2.34	0.57	0.20	6	1.5	1.15	0.33	0.21	13	2.9	1.37	0.46	0.14
Pycnonotus atriceps (BHBUL)	3	6.3	2.73	1	0	1	4.0	-	1	-	4	5.8	2.02	1	0
Stachyris erythroptera (CWBAB)	8	2.8	1.62	0.88	0.13	19	13.3	8.18	0.74	0.11	27	10.2	5.81	0.79	0.08
Trichastoma bicolor (FBAB)	17	14.1	2.96	0.88	0.08	10	24.0	10.73	1	0	27	17.8	4.36	0.93	0.05
Macronus ptilosus (FBTBAB)	4	0.5	0.29	0.50	0.29	6	14.8	7.34	1	0	10	9.1	4.84	0.80	0.13
Alophoixus bres (GCBUL)	6	8.8	3.66	0.83	0.17	4	16.5	8.95	1	0	10	11.9	4.09	0.90	0.10
Stachyris poliocephala (GHBAB)	1	21.0	-	1	-	6	4.3	3.23	0.50	0.22	7	6.7	3.62	0.57	0.20
Malacocincla sepiaria (HBAB)	9	8.1	2.66	0.89	0.11	7	5.3	3.72	0.43	0.20	16	6.9	2.16	0.69	0.12
Tricholestes criniger (HBBUL)	8	19.4	6.76	1	0	7	22.6	5.05	1	0	25	21.6	3.99	1	0
Cyornis caerulatus (LBBFLY)	5	29.8	5.67	1	0	1	0	-	0	-	6	24.8	6.79	0.83	0.17
Arachnothera longirostra (LSPHUN)	20	6.2	1.52	0.85	0.08	46	2.4	0.41	0.67	0.07	66	3.6	0.58	0.73	0.06
Malacopteron magnirostre (MBAB)	6	3.8	1.60	0.67	0.21	1	0	-	0	-	7	3.3	1.46	0.57	0.20
Ceyx rufidorsa motleyi (ODKING)	8	10.5	7.83	0.75	0.16	3	11.7	11.17	0.67	0.33	11	10.8	6.17	0.73	0.14
Hypogramma hypogrammicum (PNSUN)	16	1.3	0.36	0.63	0.13	11	0.5	0.21	0.46	0.16	27	1.0	0.24	0.56	0.10
Malacopteron magnum (RCBAB)	3	11.3	8.84	1	0	6	4.2	1.96	0.67	0.21	9	6.6	3.09	0.78	0.15
Sasia abnormis (RPIC)	8	6.4	2.04	0.88	0.13	10	3.4	0.97	0.90	0.10	18	4.7	1.08	0.89	0.08
Philentoma pyrhoptera (RWPHIL)	3	1.7	1.20	0.67	0.33	2	1.0	1.00	0.50	0.50	5	1.4	0.75	0.60	0.25
Malacopteron cinereum (SCRBAB)	11	6.2	2.11	0.82	0.12	4	1.3	0.63	0.75	0.25	15	4.9	1.64	0.80	0.11
Malacocincla malaccensis (STBAB)	13	10.6	5.04	0.69	0.13	10	5.2	1.33	0.80	0.13	23	8.3	2.91	0.74	0.09

Table 4 continue.

	Primary forest					*Logged forest*					*Overall*				
Species	**No.**	**Mean**	**SE**	**Prev.**	**SE**	**No.**	**Mean**	**SE**	**Prev.**	**SE**	**No.**	**Mean**	**SE**	**Prev.**	**SE**
Enicurus leschenaulti (WCFORK)	4	25.3	24.92	0.50	0.29	1	53.0	-	1	-	5	30.8	20.08	0.60	0.25
Copsychus stricklandi (WCSHAM)	1	145.0	-	1	-	2	23.0	18.00	1	0	3	63.7	41.97	1	0
Alophoixus phaeocephalus (YBBUL)	10	4.4	2.15	1	0	5	4.8	1.77	1	0	15	4.5	1.51	1	0
Prionochilus maculatus (YBFLPEC)	14	1.9	0.65	0.57	0.14	14	0.9	0.25	0.50	0.14	28	1.4	0.36	0.54	0.10
Grand total	**188**	**8.8**	**1.21**	**0.79**	**0.03**	**194**	**8.0**	**1.27**	**0.72**	**0.03**	**382**	**8.4**	**0.87**	**0.75**	**0.02**

Table 5: Mean intensity of ectoparasite infestation and the prevalence of ectoparasites among all sampled avian families, indicating the number of bird captures per family (No.), mean ectoparasite load (Mean), standard error (SE), and prevalence (Prev.) in each forest type and overall.

	Primary					***Logged***					***Overall***				
Family	**No.**	**Mean**	**SE**	**Prev.**	**SE**	**No.**	**Mean**	**SE**	**Prev.**	**SE**	**No.**	**Mean**	**SE**	**Prev.**	**SE**
Alcedinidae	8	10.5	7.83	0.75	0.16	3	11.7	11.17	0.67	0.33	11	10.8	6.17	0.73	0.14
Dicaeidae	14	1.9	0.65	0.57	0.14	14	0.9	0.25	0.50	0.14	28	1.4	0.36	0.54	0.10
Monarchidae	3	1.7	1.20	0.67	0.33	2	1.0	1.00	0.50	0.50	5	1.4	0.75	0.60	0.24
Muscicapidae	5	29.8	5.67	1	0.00	1	0.0	-	0	-	6	24.8	6.79	0.83	0.17
Nectariniidae	36	4.0	0.95	0.75	0.07	57	2.1	0.35	0.63	0.06	93	2.8	0.43	0.68	0.05
Picidae	8	6.4	2.04	0.88	0.13	10	3.4	0.97	0.90	0.10	18	4.7	1.08	0.89	0.08
Pycnonotidae	24	10.5	2.82	0.96	0.04	26	18.3	3.76	1	0.00	50	14.5	2.42	0.98	0.02
Timaliidae	85	8.1	1.19	0.79	0.04	78	10.1	2.60	0.72	0.05	163	9.0	1.39	0.75	0.03
Turnidae	5	49.2	30.76	0.6	0.24	3	33.0	14.42	1	0.00	8	43.1	19.21	0.75	0.16

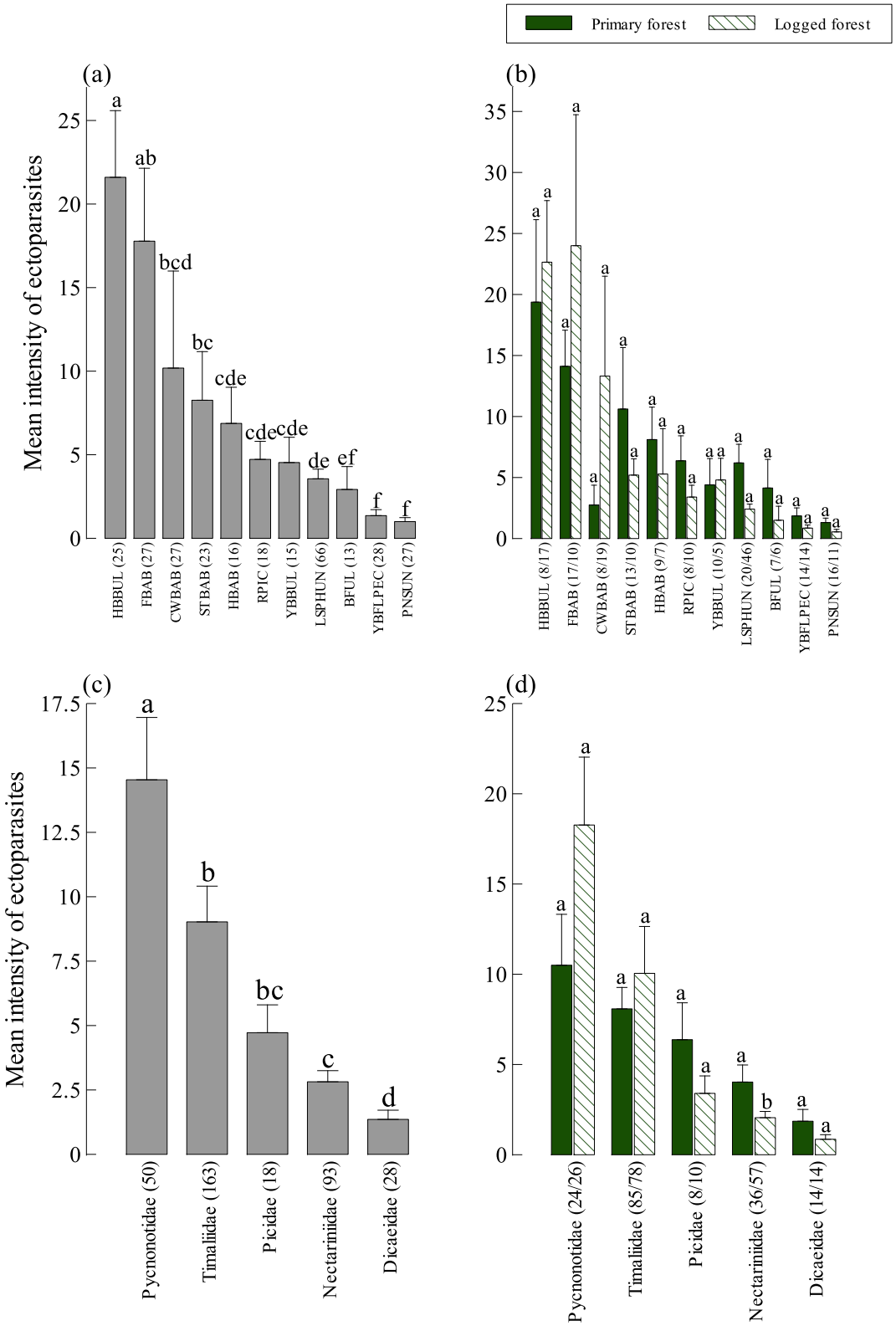

Figure 5: Mean intensity of avian ectoparasites among species and families of birds containing ≥10 in total sample size and ≥5 in each forest type; presenting (a) overall means within species, (b) means within each forest type (primary and logged forest) for species, (c) overall means within families, and (d) means within each forest type (primary and logged forest) for families. Error bars represent 1 SE. Sample sizes are given in parentheses, with (N/N) indicating sample size in primary and logged forest, respectively. Different lower case letters indicate significant differences between groups (GLMM; $p<0.05$ significance level).

3.1.4 Differences between functional and ecological traits

Feeding guild

There was a significant difference in the mean intensity of ectoparasites between feeding guilds, with all three groups differing significantly from each other (ANOVA on GLMM; $F_{2,376}$=31.19, p<0.0001; Figure 6a). Frugivores/insectivores (F,I) and insectivores (I) did not show any significant difference in ectoparasite loads between forest types, while nectarivores/insectivores (N,I) had a small, but significant decline in mean intensity of ectoparasites in logged forest (Table 6 & Figure 7a).

Foraging strategy

There was a significant overall difference in the mean intensity of ectoparasites for birds between the foraging strategies (ANOVA on GLMM; $F_{3,374}$=3.01, p=0.03). Flowerpecking birds had a significantly lower mean intensity of ectoparasites compared to the other groups; the other three groups showed little variation (Figure 6b). No groups had any significant variation between forest types (Figure 7b). Sallying birds had very few ectoparasites in logged forest compared to primary. However, as the sample group was very small, with <15 sampled in total, and only ≥5 in one forest type, this group did not allow for statistical comparison. There was an interaction present between forest types and foraging strategy groups, but this was only approaching statistical significance (ANOVA Chi-square deletion test on GLMM; Chi-square=8.10, df=4, p=0.09).

Distribution

There was a significant difference between endemic and non-endemic birds, with endemic birds having higher levels of ectoparasites (ANOVA on GLMM; $F_{1,377}$=4.25, p=0.04; Figure 6c). Non-endemic birds had a significant decline in ectoparasites in logged forest compared to primary, while endemic birds exhibited a non-significant increase in mean number of ectoparasites from primary to logged forest (Table 6 & Figure 7c). An interaction between non-endemic and endemic birds and forest types were approaching statistical significance, with the direction of difference between number of ectoparasites between primary forest and logged forest going in opposite directions for endemic and non-endemic birds (ANOVA Chi-square deletion test on GLMM; Chi-square=5.53, df=2, p=0.06).

Conservation status

Bird species considered vulnerable or threatened exhibited no difference in the mean intensity of ectoparasites compared to non-threatened species (ANOVA on GLMM; $F_{1,377}$=0.11, p=0.74; Figure 6d), with no differences between forest types (Table 6 & Figure 7d). There were no interaction between forest types and conservation status (ANOVA Chi-square deletion tests on GLMM; Chi-square=1.61, df=2, p=0.45).

Forest dependence

There was a significant overall difference in the mean intensity of ectoparasites between the forest dependence groups (ANOVA on GLMM; $F_{2,376}$=3.21, p=0.04). Primary forest dependent birds had significantly lower levels of ectoparasites (5.26 ± 1.16 SE) compared to species associated with secondary forest, or equally associated with both primary and secondary forest (9.43 ± 1.54 and 8.50 ± 1.25, respectively; Figure 6e). Primary forest dependent birds also exhibited significantly lower levels of ectoparasites in logged forest compared to primary forest (Figure 7e). The other two groups differed little across forest types. An interaction approaching statistical significance was present between forest types and the various forest dependence groups (ANOVA Chi-square deletion tests on GLMM; Chi-square=6.70, df=3, p=0.08).

Body size

There were significant overall differences in the intensity of ectoparasites between the various size groups of birds (ANOVA on GLMM; F3,375=10.72, p<0.0001), with an overall positive (linear) trend between increased body size and ectoparasite loads (Figure 6f). The effect differed between primary and logged forest (ANOVA Chi-square deletion tests on GLMM; Chi-square=14.26, df=4, p<0.01) with constantly lower intensity of ectoparasites in primary forest (Figure 7f). Nevertheless, the relationship between body size and intensity of ectoparasites was positive in both forest types (Table 6).

Table 6: Results of the GLMM models on differences in mean intensity of avian ectoparasites between forest types (primary and logged) in each subset of the functional and ecological traits. Intercepts, estimates and SE are given in log-transformed numbers. Significant p-values are marked in bold ($p<0.05$ significance level). Only the results of the linear trends (.L) are presented for body size, as no significant quadratic or cubic trends were found.

		Df	***Intercept***	***Estimate***	***SE***	***t-value***	***p-value***
Feeding guild	F,I	61	2.59	0.16	0.34	0.46	0.65
	I	190	2.23	-0.26	0.47	-0.55	0.58
	N,I	116	1.20	-0.62	0.31	-1.98	**<0.05**
Foraging strategy	Sallying	-	-	-	-	-	-
	Undergrowth	128	2.41	-0.09	0.43	-0.18	0.86
	Foliage gleaning	107	2.08	0.20	0.32	0.62	0.53
	Flowerpecking	121	1.27	-0.41	0.26	-1.54	0.12
Distribution	Endemic	243	2.10	0.06	0.36	0.15	0.88
	Non-endemic	129	2.12	-0.91	0.34	-2.68	**<0.01**
Conservation status	LC	312	2.11	-0.17	0.36	-0.48	0.63
	T	60	2.38	-0.59	0.52	-1.13	0.26
Forest dependence	Primary	60	2.04	-1.56	0.39	-3.99	**<0.001**
	Equal	133	2.10	0.06	0.36	0.15	0.88
	Secondary	173	2.37	-0.44	0.38	-1.16	0.25
	Trend	**residual df**	**Intercept**	**Estimate**	**SE**	**z-value**	**p-value**
Body size	.L (Main)	375	2.18	1.23	0.21	5.73	**<0.001**
	.L (Primary)	371	2.08	1.13	0.30	3.83	**<0.001**
	.L (Logged)	371	2.14	1.30	0.31	4.19	**<0.001**

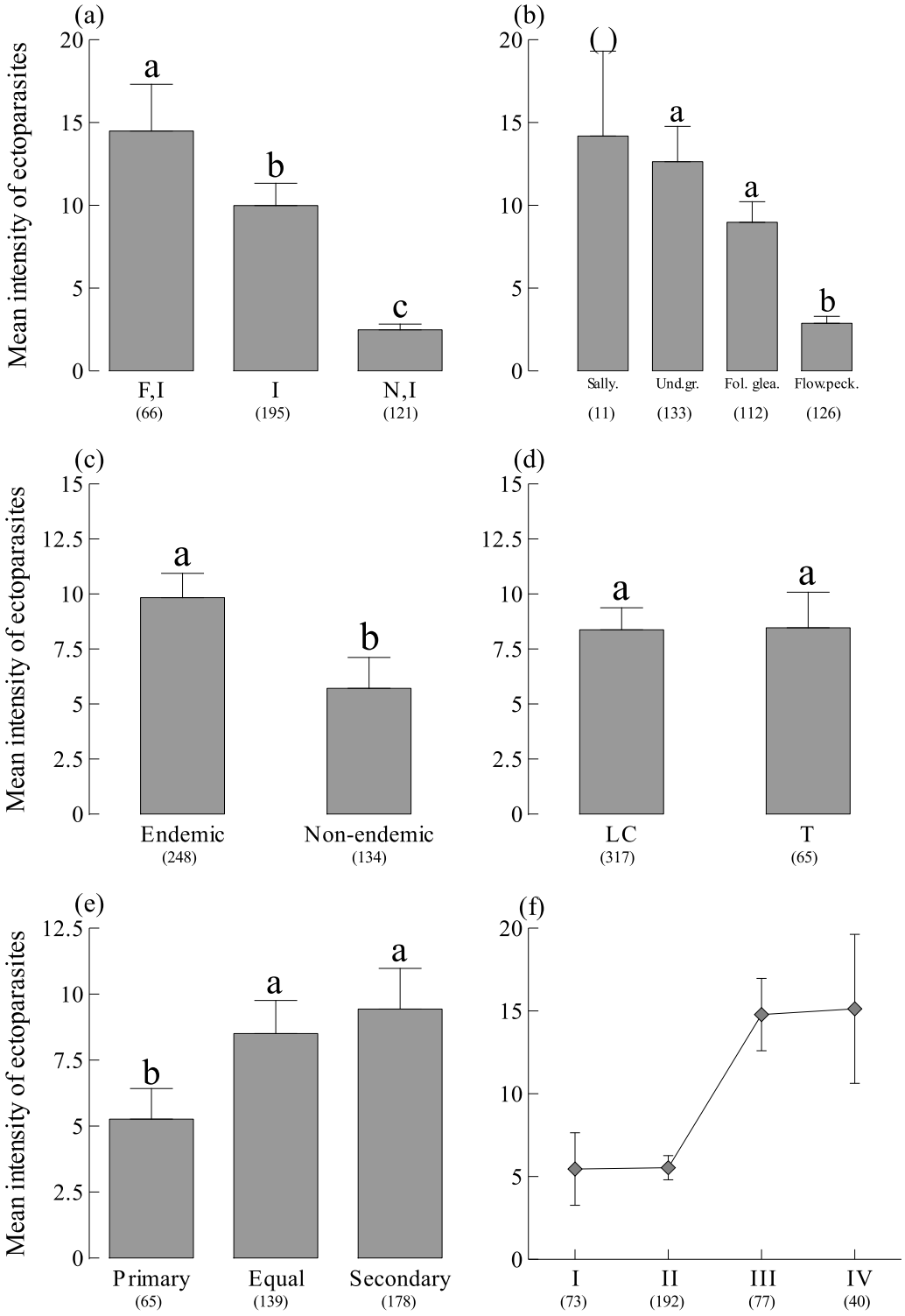

Figure 6: Mean intensity of avian ectoparasite infestations among various functional and ecological traits of birds, including (a) feeding guild, (b) foraging strategy, (c) distribution, (d) conservation status, (e) forest dependency, and (f) body size. Error bars represent 1 SE. Sample sizes are given in parentheses. Different lower case letters indicate significant differences between groups (GLMM; $p<0.05$ significance level). Empty parentheses indicate that comparisons were not possible to conduct. Abbreviations given in b): Sally.=Sallying, Und.gr.=Undergrowth, Fol.glea.=Foliage gleaning, and Flow.peck.=Flowerpecking.

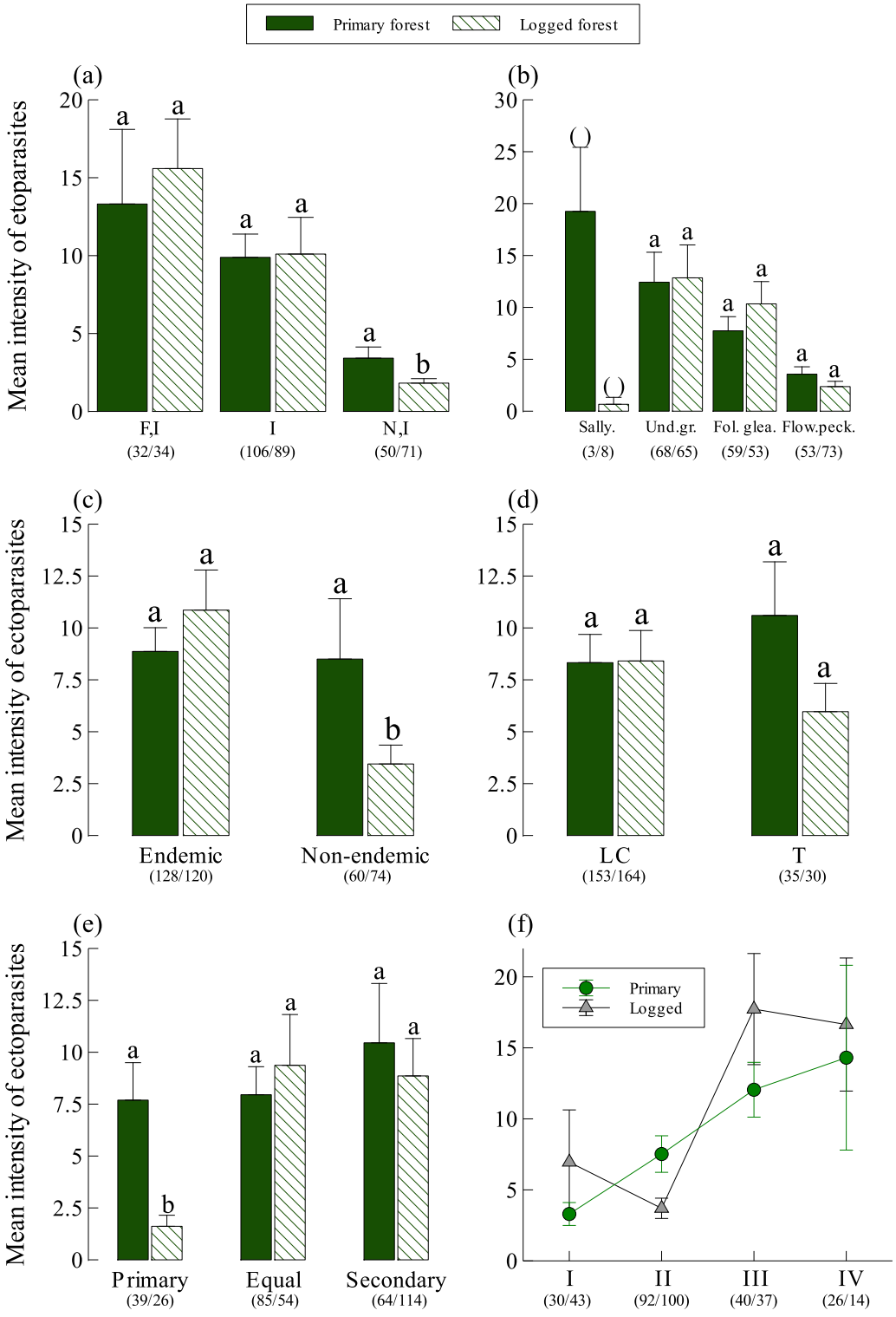

Figure 7: Mean intensity of avian ectoparasite infestations among various functional and ecological traits of birds in primary and logged forest, including (a) feeding guild, (b) foraging strategy, (c) distribution, (d) conservation status, (e) forest dependency, and (f) body size. Error bars represent 1 SE. Sample sizes are given in parentheses, with (N/N) showing sample size in primary and logged forest, respectively. Different lower case letters indicate significant differences between forest types within groups (GLMM; $p<0.05$ significance level). Empty parentheses indicate that comparisons were not possible to conduct. Abbreviations given in b): Sally.=Sallying, Und.gr.=Undergrowth, Fo.glea.=Foliage gleaning, and Flow.peck.=Flowerpecking.

3.1.5 Correlation with body condition

Eight birds had fully developed pectoral muscles, scoring '3' on the muscle index, while the rest were evenly distributed between undeveloped pectoral muscles and slightly rounded well-developed muscles, scoring '0', '1', and '2'. All but two individual birds had very little fat storage (fat index scores '0', '1', and '2'), with no birds scoring any higher than '3'. Statistical analysis was thus conducted firstly with all levels included, and then with only the levels with ≥10 in sample size, thus excluding level '3' for muscle scores and level '3' for fat scores (with fat score '4' and '5' not registered). Wing length did not converge in maximum iterations and could not be analysed.

There was no relationship between ectoparasite numbers and muscle score (ANOVA on GLMM; $F_{2,351}$=0.65, p=0.52). A significant (linear) increase in mean ectoparasite intensity with increasing muscle scores was found when all samples were included, but this became non-significant when the highest level of muscle score (score '3'), which had very low sample size, was excluded (Table 7 & Figure 8a). No significant trends were found in either primary or logged forest (Table 7 & Figure 8b), with no interaction between forest types and muscle score (ANOVA Chi-square deletion test on GLMM; Chi-square=1.51, df=3, p=0.68). Fat scores showed similar pattern (Figure 8c), with no relationship between ectoparasite intensity and fat score found (ANOVA on GLMM; $F_{2,357}$=1.68, p=0.19). However, no overall significant trends were found when testing all samples pooled, while a small non-linear trend was found closing on statistical significance when testing without score '3' (Table 7). This was created by a significant positive (non-linear) trend within logged forest, while no trends were found in primary forest (Figure 8d). There were no interaction between forest type and fat score (ANOVA Chi-square deletion test on GLMM; Chi-square=3.14, df=3, p=0.37).

Table 7: Results of the GLMM models on differences in mean intensity of avian ectoparasite infestations between forest types (primary and logged) in the body condition measurements muscle score and fat score. Intercepts, estimates and 1 SE given in log-transformed numbers. The results of the linear trend are given for all groups, while the non-linear trends are given only for fat scores, as none significant was present for muscle score. Main models run with and without score '3' are shown, while only the models without score '3' are shown for each forest type. Significant p-values are marked in bold ($p<0.05$ significance level). The test for fat score in primary forest did not converge.

	Trend	***Intercept***	***Estimate***	***SE***	***z-value***	***p-value***
Muscle score						
Main effect	.L	2.12	0.73	0.34	2.14	**0.03**
Main effect (excl. "3")	.L	1.89	0.18	0.16	1.10	0.27
Primary (excl. "3")	.L	2.04	0.20	0.22	0.88	0.38
Logged (excl. "3")	.L	1.73	0.12	0.20	0.58	0.56
Fat score						
Main effect	.L	1.93	-0.03	0.63	-0.05	0.96
Main effect (excl. "3")	.L	1.88	-0.12	0.23	-0.50	0.62
	.Q	1.88	-0.34	0.21	-1.65	0.10
Primary (excl. "3")	.L	-	-	-	-	-
Logged (excl. "3")	.L	1.67	-0.29	0.36	-0.80	0.42
	.Q	1.67	-0.61	0.29	-2.14	**0.03**

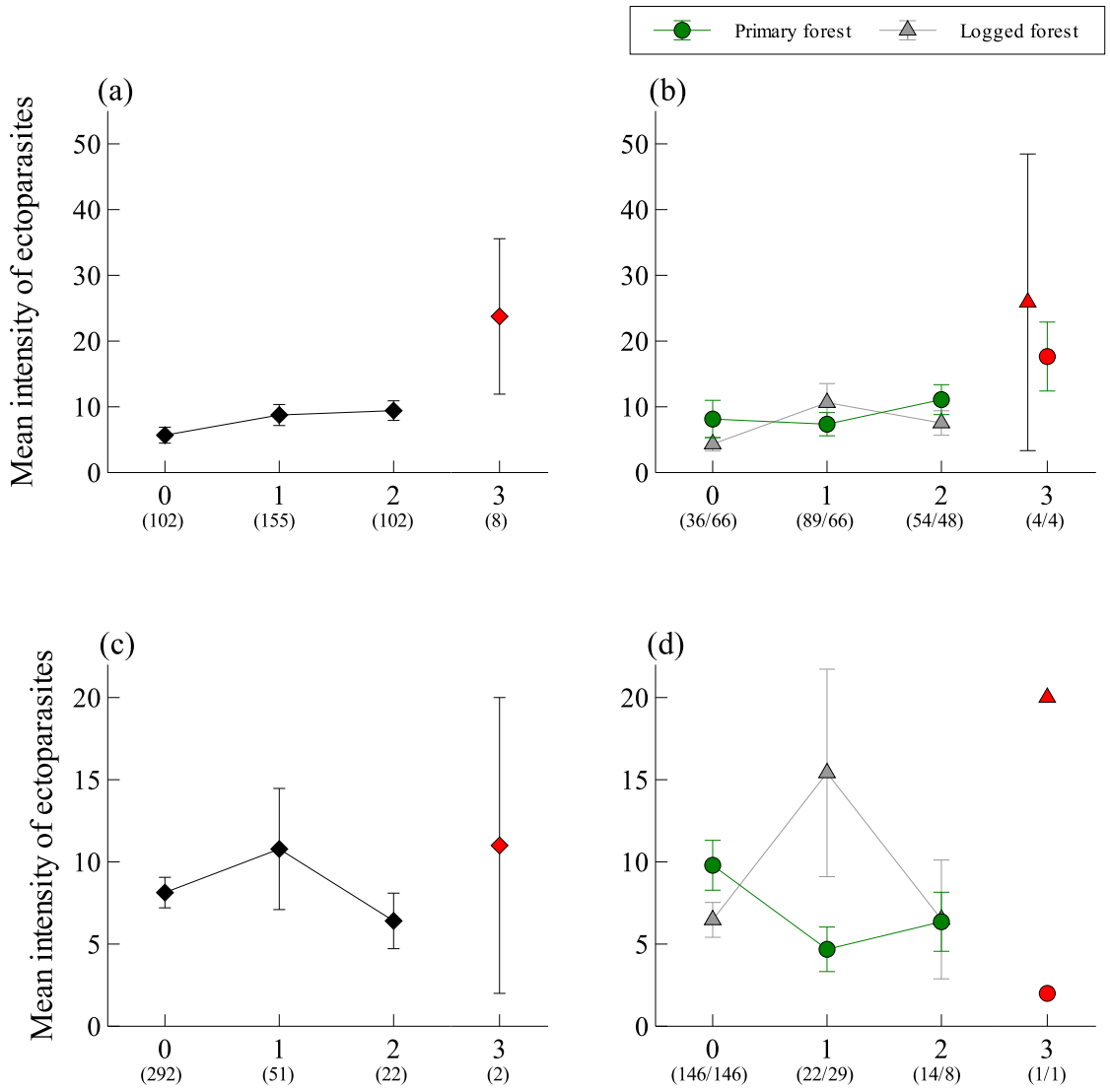

Figure 8: Mean intensity of ectoparasite infestation among birds recorded in the different (a) muscle and (c) fat score categories, and the differences in ectoparasite load between forest types within (b) muscle and (d) fat scores. Error bars represent 1 SE. Sample sizes are given in parentheses, with (N/N) indicating sample size in primary and logged forest, respectively. Score '3' is outlined in red and not included in trend lines, as test were done both with and without score '3'. Score '3' in d) have no error bars, as only 1 sample existed within each forest type.

3.2 Blood parasites

3.2.1 Distribution of blood parasites

Of the 258 birds examined, 41 (15.9%) were infected with blood parasites: 36 (14%) were infected with *Haemoproteus*, 1 (0.4%) with *Plasmodium*, and 4 (1.6%) with microfilariae. No birds were found infected with *Trypanosoma* or *Leucocytozoon*. The one registration of *Plasmodium* and the four samples with microfilariae were all found in one bird species, *Trichastoma bicolor* (FBAB).

3.2.2 Differences between primary and logged forest

There was no significant difference between the prevalence of blood parasites in primary (0.13 ± 0.03, N=128) and logged (0.19 ± 0.03, N=130) forest ($F\text{-value}_{1,252}=2.70$, p-value=0.10). The difference of 13% infected in primary and 19% in logged, constitute an increase of 50% from primary to logged forest.

3.2.3 Differences between species and families

Species containing <10 samples in total and <5 in each forest type were excluded from the analysis of species, and are not presented in the figures. One family with a sample size of <10 was excluded from the analysis, and likewise were families or species with zero prevalence, as they created complete separation in the models. This left 9 species and 4 families for analysis between forest types.

The prevalence of blood parasites across species did not differ significantly (ANOVA on GLMM; $F_{8,127}=0.81$, P=0.60). However, some significant differences in the prevalence of blood parasites were found (Figure 9). Of the 18 avian species sampled for blood parasites, 11 had detectable infections, while 7 did not show any sign of infection. The prevalence within the infected species varied considerably, with some species having very few individuals infected, even with larger sample sizes, like *Malacopteron cinereum* (SCRBAB), while others had a high percentage of infected invididuals, like *Trichastoma bicolor* (FBAB) and *Copsychus stricklandi* (WCSHAM) (Table 8 & Figure 9). There was a significant interaction between forest type and species (ANOVA Chi-square deletion test on GLMM; Chi-square=18.07, df=9, p=0.03), but no significant differences between forest types were found within any of the species.

There were significant differences in prevalence between the families (ANOVA on GLMM; $F_{3,190}$=4.05, p<0.01), with *Timaliidae* having a significantly lower prevalence than *Pycnonotidae* and *Turnidae* (Figure 9c). *Pycnonotidae* differed across forest types, having significantly higher prevalence in logged forest, while the other families differed little (Table 9 & Figure 9). The overall effect of family also depended on forest type, with a significant interaction (ANOVA Chi-square deletion test on GLMM; F=12.93, df=4, p=0.01).

Table 8: Total number of birds of each species with blood sampled and the number of individuals infected with blood parasites in primary and logged forest, and overall, presented with the overall prevalence and 1 SE.

	Primary forest		***Logged forest***		***Overall***			
Species	**Infected**	**Total**	**Infected**	**Total**	**Infected**	**Total**	**Prevalence**	**SE**
Alcippe brunneicauda (BFUL)	1	5	2	10	3	15	0.20	0.11
Stachyris maculata (CRBAB)	0	3	0	5	0	8	0.0	NA
Stachyris erythroptera (CWBAB)	0	5	0	12	0	17	0.0	NA
Trichastoma bicolor (FBAB)	2	7	4	6	6	13	0.46	0.14
Macronus ptilosus (FBTBAB)	0	2	0	8	0	10	0.0	NA
Alophoixus bres (GCBUL)	0	5	2	3	2	8	0.25	0.16
Malacocincla sepiaria (HBAB)	2	11	0	6	2	17	0.12	0.08
Tricholestes criniger (HBBUL)	1	9	6	11	7	20	0.35	0.11
Arachnothera longirostra (LSPHUN)	0	16	0	22	0	38	0.0	NA
Ceyx rufidorsa motleyi (ODKING)	0	4	0	3	0	7	0.0	NA
Malacopteron magnum (RCBAB)	1	5	1	3	2	8	0.25	0.16
Sasia abnormis (RPIC)	0	5	0	8	0	13	0.0	NA
Malacopteron cinereum (SCRBAB)	0	12	1	6	1	18	0.06	0.06
Malacocincla malaccensis (STBAB)	3	10	0	7	3	17	0.18	0.10
Enicurus leschenaulti (WCFORK)	0	1	0	1	0	2	0.0	NA
Copsychus stricklandi (WCSHAM)	3	6	4	8	7	14	0.50	0.14
Alophoixus phaeocephalus (YBBUL)	1	9	3	5	4	14	0.29	0.13
Prionochilus maculatus (YBFLPEC)	3	13	1	6	4	19	0.21	0.10
Grand Total	17	128	24	130	41	258	0.16	0.02

Table 9: Results of the GLMM models on differences in avian blood parasite prevalence between forest types (primary and logged) within the species and families with overall sample size ≥10 and ≥5 in each forest type. Only species and families for which the analysis could be performed are presented. Intercepts, estimates and 1 SE given in logit-transformed numbers. Significant p-values are marked in bold (p<0.05 significance level).

	Df	***Intercept***	***Estimate***	***SE***	***t-value***	***p-value***
Species						
Copsychus stricklandi (WCSHAM)	10	-3.96E-08	9.04E-08	1.08	0	1
Trichastoma bicolor (FBAB)	9	-0.92	1.61	1.20	1.34	0.18
Tricholestes criniger (HBBUL)	16	-2.35	2.68	1.71	1.57	0.12
Alophoixus phaeocephalus (YBBUL)	10	-2.08	2.49	1.40	1.78	0.08
Prionochilus maculatus (YBFLPEC)	15	-1.45	-0.24	1.70	-0.14	0.89
Alcippe brunneicauda (BFUL)	11	-1.39	6.32E-12	1.37	0	1
Family						
Pycnonotidae	190	-2.38	2.85	1.04	2.74	**0.01**
Timaliidae	190	-1.76	-0.22	0.59	-0.37	0.72
Turnidae	190	-0.32	0.16	1.11	0.15	0.88
Dicaeidae	190	-1.23	-0.56	1.37	-0.41	0.68

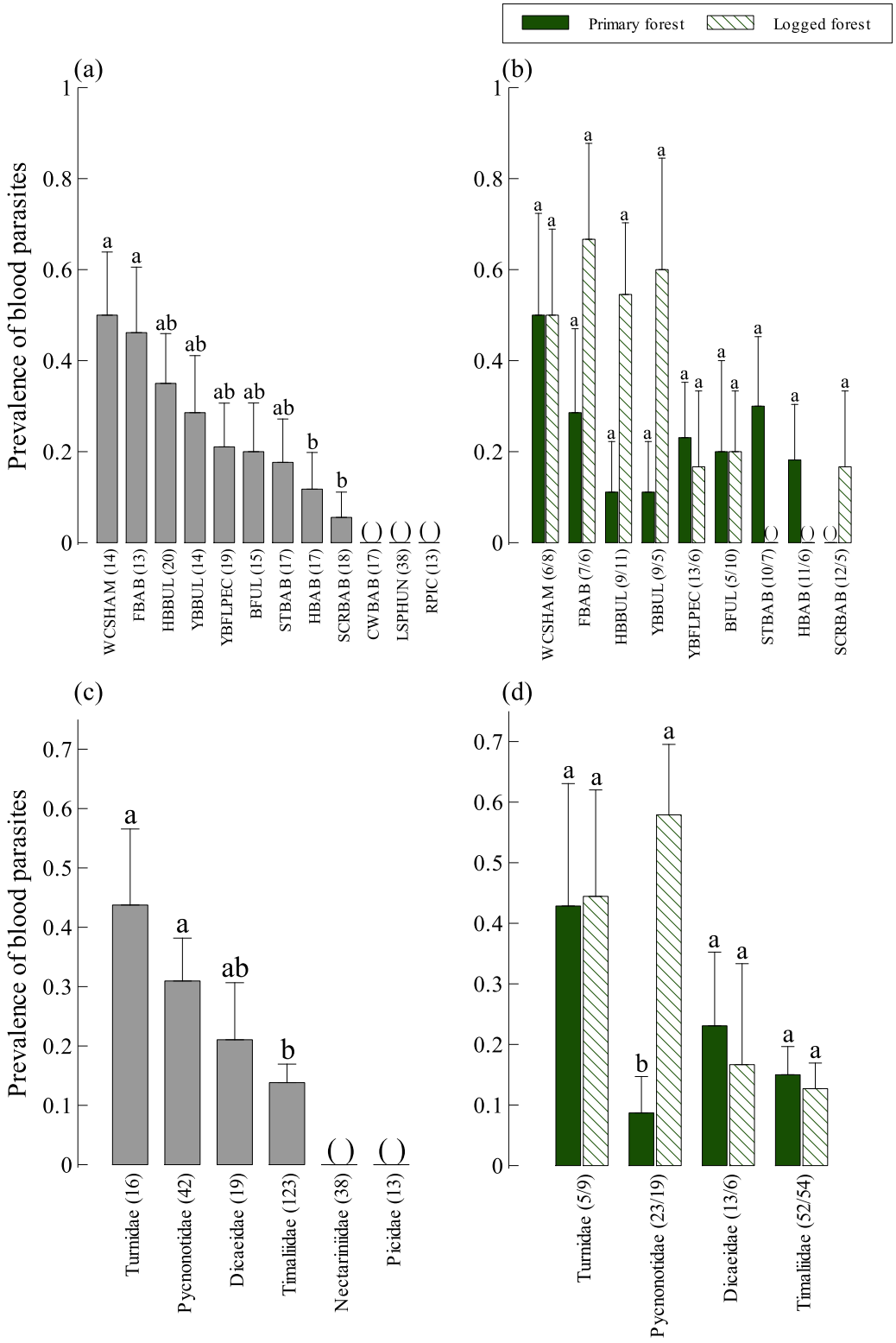

Figure 9: Prevalence of avian blood parasites among species and families of birds containing ≥10 in total sample size and ≥5 in each forest type; presenting (a) overall prevalence within species, (b) prevalence within each forest type (primary and logged forest) for each species, (c) overall prevalence within families, and (d) prevalence within each forest type (primary and logged forest) for each family. Error bars represent 1 SE. Sample sizes are given in parentheses, with (N/N) indicating sample size in primary and logged forest, respectively. Different lower case letters indicate significant differences between groups (GLMM; $p<0.05$ significance level). Empty parentheses indicates that comparisons were not possible.

3.2.4 Differences between functional and ecological traits

Feeding guild

There was a significant difference in prevalence between the feeding guilds (ANOVA on GLMM; $F_{2,250}$=7.45, p<0.001), and a significant interaction with forest types (ANOVA Chi-square deletion test on GLMM; Chi-square=8.06, df=3, p=0.04). Frugivores/insectivores (F,I) had a significantly higher prevalence of blood parasites compared to insectivores (I) and nectarivores/insectivores (N,I; Figure 10). This was mainly caused by the high prevalence of blood parasites for frugivores/insectivores in logged forest. They had more than twice as high prevalence in logged forest compared to primary (0.18 ± 0.07 and 0.46 ± 0.08, respectively; Table 10), while the other feeding guilds varied little (Figure 11).

Foraging strategy

The various foraging strategy groups did not differ significantly overall (ANOVA on GLMM; $F_{2,250}$=0.19, p=0.20), but foliage gleaning birds had a significantly higher prevalence of blood parasites compared to flowerpeckering birds (Figure 10). There was a significant interaction effect between foraging strategy and forest type (ANOVA Chi-square deletion test on GLMM; Chi-square=11.29, df=3, p=0.01). Foliage gleaners had significantly higher prevalence of blood parasites in logged forest compared to primary forest (0.08 ± 0.04 and 0.33 ± 0.07, in primary and logged forest, respectively; Table 10 & Figure 11).

Distribution

Non-endemic birds had slightly lower levels of blood parasites compared to endemic birds (0.09 ± 0.03 and 0.19 ± 0.03, non-endemic and endemic, respectively; Figure 10), with an overall significant difference (ANOVA on GLMM; $F_{1,254}$=3.83, p=0.05). Both groups trended towards higher prevalence in logged forest compared to primary, although this was non-significant (Table 10 & Figure 11). There was no significant interaction between distribution and forest type (Chi-square deletion test on GLMM; Chi-square=1.49, df=2, p=0.47).

Conservation status

There was no difference in the blood parasite prevalence among non-threatened and threatened birds (ANOVA on GLMM; $F_{1,252}$=0.05, P=0.82; Figure 10). Non-threatened species had a

significantly higher prevalence of blood parasites in logged forest compared to primary, while threatened species had lower, but non-significant prevalence in logged forest compared to primary (Table 10 & Figure 11). The interaction term was only approaching statistical significance (ANOVA Chi-square deletion test on GLMM; Chi-square=5.07, df=2, p=0.08).

Forest dependence

No differences in blood parasite prevalence were found between birds of species preferring primary forest, secondary forest or those that equally utilise both forest types (ANOVA on GLMM; $F_{2,253}$=1.78, p=0.17; Figure 10). None of the groups exhibited any differences between forest types (Table 10 & Figure 11), with no interaction with forest type (ANOVA Chi-square deletion test on GLMM; Chi-square=2.58, df=3, p=.46).

Body size

There were significant differences in the prevalence of blood parasites between the different body size groups (ANOVA on GLMM; F3,248=5.61, p<0.001), with a significant (non-linear) increase in blood parasite prevalence with increasing body weight (Table 10). The interaction between forest type and body size was also significant (ANOVA Chi-square deletion test on GLMM; Chi-square=11.93, df=4, p=0.02), clearly shown by the differences in blood parasite prevalence between primary and logged forest within the body size groups (Figure 11). There were no trends found in primary forest, while there were positive (linear and a non-linear) trends in logged forest with a high increase in prevalence in size classes III and IV compared to I and II (Table 10).

Table 10: Results of the GLMM models on differences in avian blood parasite prevalence between forest types (primary and logged) in subset of the functional and ecological traits. Intercepts, estimates and 1 SE are given in logit-transformed numbers. Significant p-values are marked in bold (p<0.05 significance level). The results of the linear trends (.L) are presented for body size, both overall, and for primary and logged forest separately, as well as significant cubic trends.

		Df	***Intercept***	***Estimate***	***SE***	***t-value***	***p-value***
Feeding guild	F,I	250	-1.54	1.38	0.60	2.32	**0.02**
	I	250	-1.96	-0.32	0.58	-0.56	0.58
	N,I	250	-2.16	-1.14	1.24	-0.92	0.36
Foraging strategy	Foliage gleaning	250	-2.44	1.72	0.61	2.82	**<0.01**
	Undergrowth	250	-1.36	-0.43	0.52	-0.83	0.41
	Flowerpecking	250	-2.16	-1.14	1.19	-0.96	0.34
Distribution	Endemic	169	-1.67	0.42	0.39	1.07	0.28
	Non-endemic	81	-2.77	0.37	1.39	0.26	0.79
Conservation status	LC	252	-2.03	0.74	0.38	1.90	**0.05**
	T	252	-1.39	-0.92	0.79	-1.17	0.24
Forest dependence	Primary	41	-1.87	0.49	0.84	0.58	0.56
	Equal	72	-1.56	0.71	0.58	1.23	0.22
	Secondary	133	-2.30	0.18	0.75	0.24	0.81
	Trends	**Df**	**Intercept**	**Estimate**	**SE**	**z-value**	**p-value**
Body size	.L (overall)	252	-1.61	1.57	0.43	3.64	0.11
	.C (overall)	252	-1.61	-0.75	0.34	-2.21	**0.03**
	.L (primary)	248	-1.79	0.43	0.58	0.75	0.45
	.L (logged)	248	-1.58	2.85	0.77	3.68	**<0.001**
	.C (logged)	248	-1.58	-1.09	0.54	-2.01	**0.04**

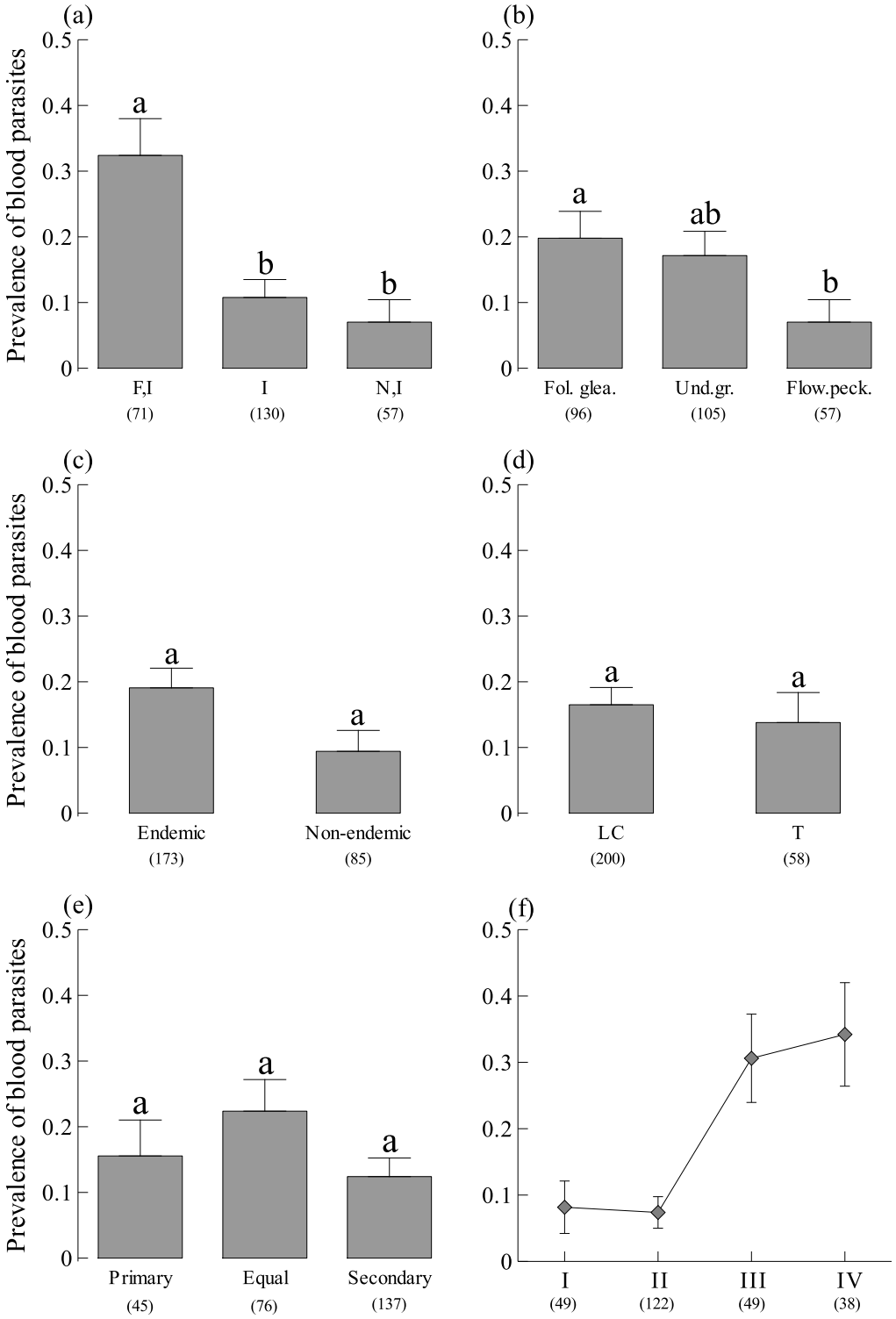

Figure 10: Prevalence of avian blood parasites among various functional and ecological traits of birds, including (a) feeding guild, (b) foraging strategy, (c) distribution, (d) conservation status, (e) forest dependency, and (f) body size. Error bars present 1 SE. Sample sizes are given in parentheses. Different lower case letters indicate significant differences between groups (GLMM; $p<0.05$ significance level). Abbreviations given in b): Fol.glea.= foliage gleaning, Und.gr.= Undergrowth, Flow.peck.= Flowerpecking.

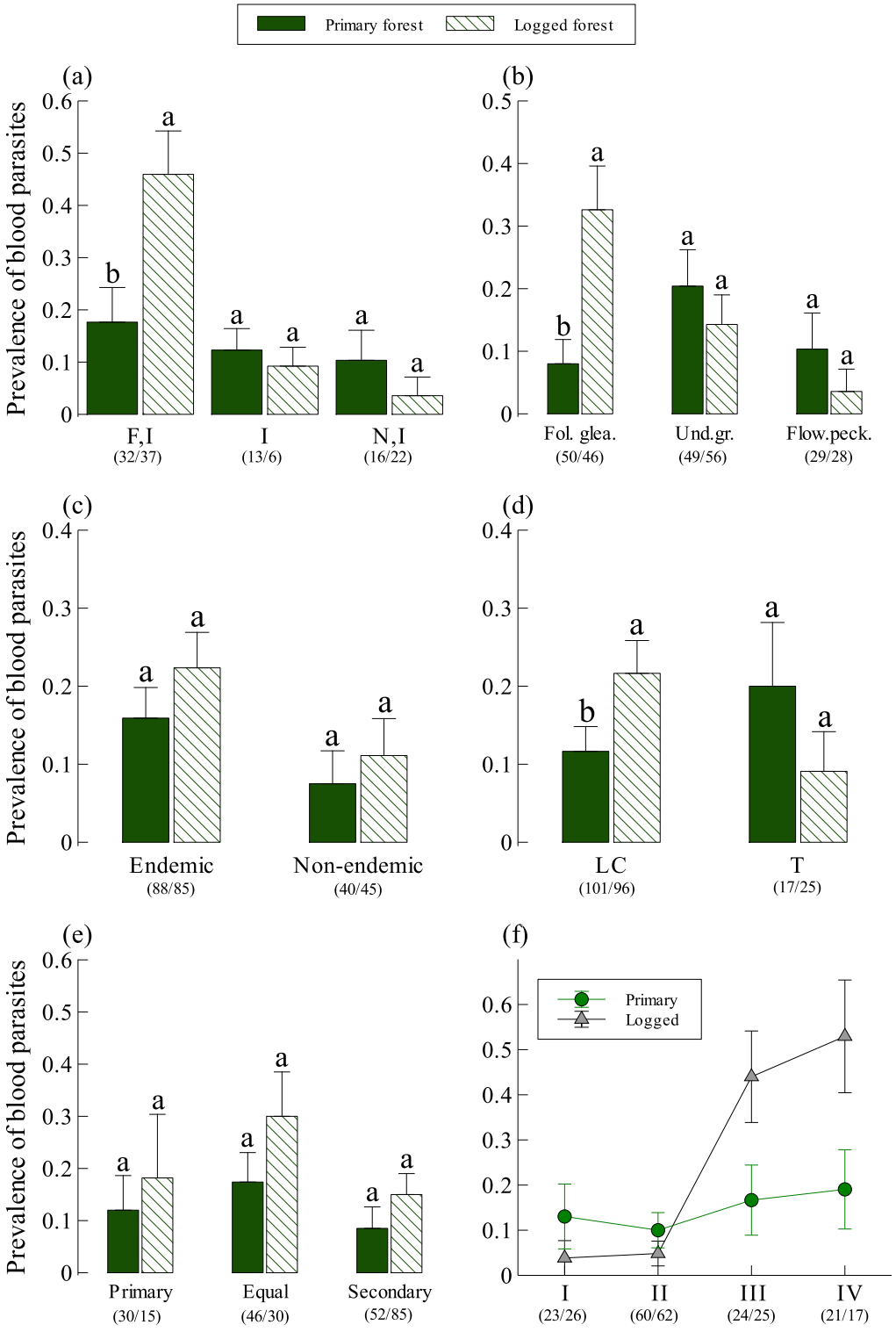

Figure 11: Prevalence of avian blood parasites among various functional and ecological traits of birds in primary and logged forest, including (a) feeding guild, (b) foraging strategy, (c) distribution, (d) conservation status, (e) forest dependency, and (f) body size. Error bars represent 1 SE Sample sizes are given in parentheses, with (N/N) showing sample size in primary and logged forest, respectively. Different lower case letters indicate significant differences between forest type within groups (GLMM; $p<0.05$ significance level). Abbreviations given in b): Fol.glea.= foliage gleaning, Und.gr.= Undergrowth, Flow.peck.= Flowerpecking.

3.2.5 Correlation with body condition

The birds were evenly distributed within the muscle score '0', '1' and '2', while only eight scored '3'. The distribution within fat scores were even more skewed. More than ¾ scored '0', having no visible fat storage, only two scored '3', and none scored higher (Figure 12). The groups of zero prevalence did not associate in the tests, thus the results with score '3' had to be excluded overall for fat score, and for primary forest for muscle score. Wing length did not converge in maximum iterations and could not be analysed.

The prevalence of blood parasites showed no differences between muscle scores (ANOVA on GLMM; $F_{3,249}$=0.50, p=0.68, all scores, and $F_{2,245}$=0.68, p=0.51, excluding score '3'), with no significant trends overall, or within the forest types (Table 11), and no interaction effect with forest types were found (ANOVA Chi-square deletion test on GLMM; Chi-square=3.35, df=4, p=0.50, all scores, and Chi-square=2.91, df=3, p=0.41, excluding score '3'). There were no differences in prevalence of blood parasites within fat scores (ANOVA on GLMM; $F_{2,247}$=0.63, p=0.53). No significant overall trends were found, or within the forest types (Table 11). No interaction effect with forest types was found (ANOVA Chi-square deletion test on GLMM; Chi-square=5.30, df=3, p=0.15).

Table 11: Results of the GLMM models on differences in avian blood parasite prevalence between forest types (primary and logged) in the body condition measurements muscle scores and fat scores. Intercepts, estimates and 1 SE given in logit-transformed numbers. The results of the linear trend are given for all groups, while the non-linear trends are given only for fat scores. Main models run with and without score 3 are both shown, while only the models without score 3 are shown for each forest type. Significant p-values are marked in bold ($p<0.05$ significance level). The full model of fat score did not converge.

	Trend	***Intercept***	***Estimate***	***SE***	***z-value***	***p-value***
Muscle scores						
Main effect	.L	-2.02	0.09	0.88	0.11	0.92
Main effect (excl. "3")	.L	-2.03	0.18	0.36	0.50	0.62
Primary (excl. "3")	.L	-2.40	0.16	0.58	0.28	0.78
Logged (excl. "3")	.L	-1.77	0.32	0.48	0.67	0.50
Fat scores						
Main effect	.L	-	-	-	-	-
Main effect (excl. "3")	.L	0.003	0.01	0.02	0.42	0.67
Primary (excl. "3")	.L	-1.73	0.09	0.58	0.15	0.88
Logged ("excl. "3")	.L	-2.62	0.32	0.65	0.50	0.62

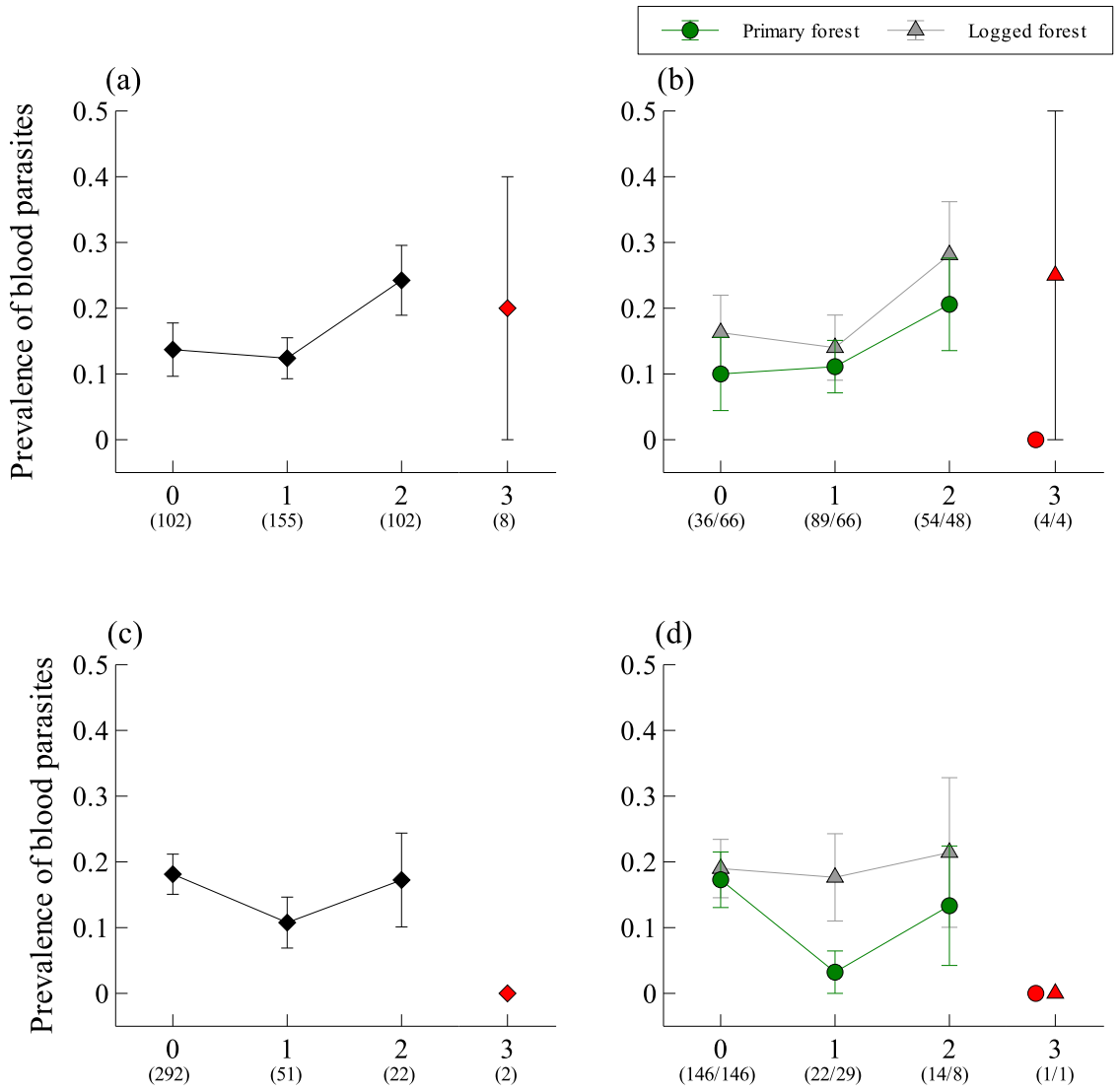

Figure 12: Prevalence of blood parasites among birds recorded in the different (a) muscle and (c) fat score categories, and the differences in prevalence between forest types within (b) muscle and (d) fat scores. Error bars represent 1 SE. Sample sizes are given in parentheses, with (N/N) indicating sample size in primary and logged forest, respectively. Score '3' are outlined in red and not included in trend line, as tests were done both with and without score '3'.

3.3 Correlation between ectoparasites and blood parasites

Birds infected with blood parasites were found to have a significantly higher intensity of ectoparasites compared to birds not infected with blood parasites (GLMM; z=2.29, p=0.02). Birds that tested negative for blood parasites had a mean intensity of 10.8 ± 1.8 ectoparasites, while birds that tested positive for blood parasites had 14.3 ± 3.2 ectoparasites on average (Figure 13). The prevalence of ectoparasites was also higher in the birds found infected with blood parasites compared to those without infection (0.96 ± 0.04 and 0.81 ± 0.03, for positive and negative of blood parasite samples, respectively), but only approaching statistical significance (ANOVA on GLMM; $F_{1,158}$=3.18, p=0.07).

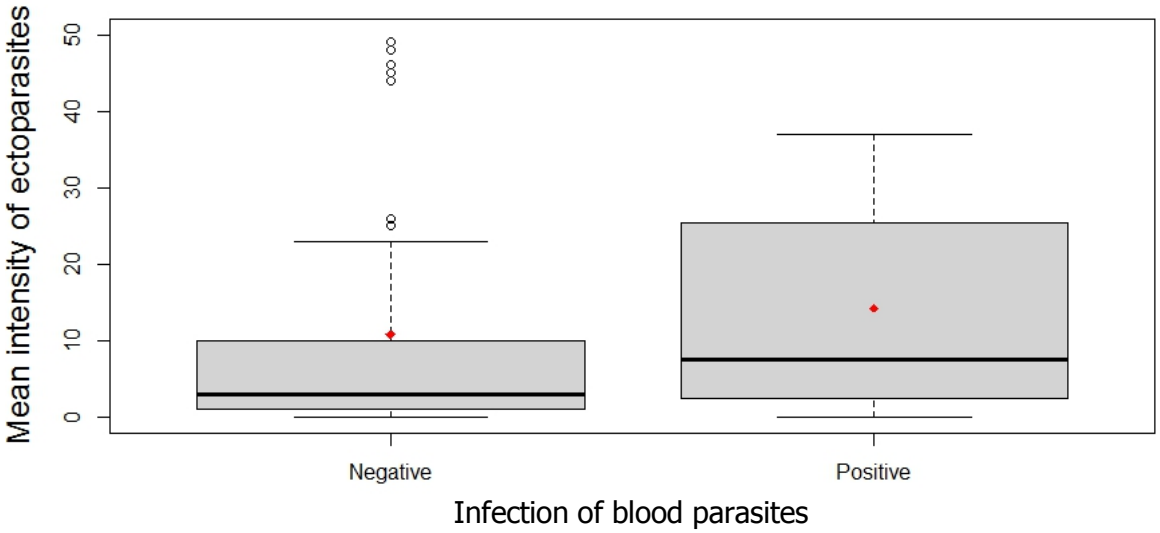

Figure 13: Mean intensity of ectoparasite infestation in birds that tested either negative or positive for blood parasites. The grey boxes encompass the interquartile range (IQR), with the horizontal line indicating the median and whiskers showing the location of ±1.58 IQR. Suspected outliers are shown as white dots above the whiskers and the means are shown in red diamonds. The graph is limited to y=50. The extreme measurements of >50 ectoparasites are thus not included in the display.

3.4 Correlation between body condition measurements

Muscle scores and fat scores were not correlated (Kendall tau rank sum test; tau= -0.07, z= -1.72, p= 0.09). Wing length on the other hand, was weakly correlated with both muscle scores (Kendall tau rank sum test; tau= 0.10, z= 2.09, p= 0.04) and fat scores (Kendall tau rank sum test; tau= -0.11, z= -2.20, p= 0.03). The results vary, when analysing within each of the species with ≥15 in sample size (Table 12). Muscle and fat scores were positively correlated for *Arachnothera longirosta* (LSPHUN) and *Alcippe brunnicauda* (BFUL), while they were negatively correlated for *Malacocincla malaccencis* (STBAB) and *Stachyris erythroptera* (CWBAB). Wing length and fat scores were significantly correlated for *Malacopteron cinereum* (SCRBAB) (Table 12).

Median wing length was similar between logged and primary forest (Table 13). Fat scores gave similar results, while muscle scores were significantly lower in logged forest (Table 13).

Table 12: Intercorrelation matrix for the body condition measurements wing length (WL), muscle score (MS) and fat score (FS) within species with sample size ≥15. Asterisks denote significance levels in Kendall's tau rank correlation analysis (*=p<0.05, **=p<0.01, ***=p<0.001), with Tau correlation coefficient given.

	WL	***MS***
Arachnotera longirosta (LSPHUN)		
MS	0.08	
FS	-0.08	0.41***
Tricholestes criniger (HBBUL)		
MS	0.35	
FS	-0.22	-0.22
Prionochilus maculatus (YBFLPEC)		
MS	-0.13	
FS	-0.12	-0.02
Malacocincla malaccensis (STBAB)		
MS	0.38	
FS	-0.36	-0.46*

	WL	***MS***
Malacocincla sepiaria (HBAB)		
MS	-0.19	
FS	0	-0.05
Stachyris erythroptera (CWBAB)		
MS	-0.25	
FS	0.10	-0.57**
Malacopteron cinereum (SCRBAB)		
MS	-0.12	
FS	-0.57**	-0.18
Alcippe brunnicauda (BFUL)		
MS	0.26	
FS	-0.08	0.50*

Table 13: Results of Kruskall-Wallis rank sum tests for differences in body condition measurements between forest types (primary and logged). Changes in mean wing length (WL, in mm), fat score (FS) and muscle score (MS) exhibited. Significant p-values are marked in bold (p<0.05 significance level).

	Change primary to logged	*Chi-square value*	*p-value*
WL~Forest type	+0.12	0.05	0.83
FS~Forest type	+0.14	0.46	0.50
MS~Forest type	-0.12	4.98	**0.03**

4. Discussion

4.1 Comparison of the recorded parasite prevalence and intensity to other studies

Feather mites were found on more than 69% of the birds sampled, although most birds only hosted a relatively small load. This is consistent with other studies on feather mites, where the prevalence have been found as 60-80% (Behnke et al. 1995; Blanco et al. 1999; Enout et al. 2012). Contrastingly, only 10% of birds were found infected with lice in this study, which is significantly lower than the average prevalence of 45% recorded in other studies (Bush et al. 2013; Clayton et al. 1992). This difference may be due to different methods used for lice quantification, as other studies have relied on visual counts of lice on wing feathers or full body inspection *post mortem,* and not dust-ruffling as in this study. Dust-ruffling is considered to only obtain a small amount of the actual ectoparasite load of the bird (Walther & Clayton 1997). The removal rates are particularly low for groups such as ticks and lice (Koop & Clayton 2013). Koop and Clayton (2013) suggested that bird body size may affect the removal rates of lice with dust ruffling, postulating that smaller birds are more difficult to dust-ruffle properly. This may explain the low numbers of lice obtained in this study, as almost all dust-ruffled species were birds smaller than the Common Starling (*Sturnus vulgaris*) (mean body size 21cm; del Hoyo 2014) tested in the study of Koop and Clayton (2013). Other ectoparasite groups, such as fleas, are usually absent in dust-ruffling samples, as they are very agile and will usually abandon their host within a short time after bird capture (Clayton & Walther 1997).

The prevalence of blood parasites was 15.9%, which falls well within the prevalence levels recorded for other tropical areas. A review of avian blood parasites from Southern Asia concluded with an overall prevalence of 16.3% (McClure et al. 1973) and birds of the Neotropics have been recorded with somewhat lower overall prevalence (10.5 %; White et al. 1978). The overall prevalence of blood parasites in European passerine birds, on the other hand, have been recorded as 26% in a review by (Scheuerlein & Ricklefs 2004), and even higher overall prevalence (36.9%) have been recorded in birds breeding in North America (Greiner et al. 1975). However, the prevalence of blood parasites vary greatly between locations within each region, and range between 1.4% to 19.0% in the Neotropics (Benedikt et al. 2009; Bennett & Lopes 1980; Bennett et al. 1991; Woodworth-Lynas et al. 1989) and between 7.0% to 30% in Southeast Asia (Elahi et al. 2014; Murata 2002; Paperna et al. 2008). In this study, 14.0% were infected with *Haemoproteus*, 1.6% with microfilariae and 0.4% with *Plasmodium*.

Leucocytozoon and *Trypanosoma* were not recorded. This is very close to the frequencies recorded in Sarawak and Java (Paperna et al. 2008). As many avian species are shared between Java, Sarawak and Sabah (Phillipps & Phillipps 2009), it is reasonable to assume that both the prevalence and the relative frequencies of the different blood parasite genera may be similar. The absence of infection of *Leucocytozoon* is consistent with findings from other tropical regions, as *Leucocytozoon* seem to be scarce in tropical rainforest habitats, with the exception of montane regions (Paperna et al. 2005; Sehgal et al. 2005; White et al. 1978). This is consistent with the distribution of black flies of the family *Simuliidae*, which are known vectors of *Leucocytozoon*. Higher species richness of *Simuliidae* has been recorded from temperate region compared to tropical (Hamada et al. 2002; McCreadie et al. 2005). Furthermore, in tropical regions, higher abundance and species richness of black flies are connected to larger and cooler streams in montane habitats (Coscarón & Coscarón-Arias 1995; Hamada et al. 2002; McCrae 1969; Rodríguez et al. 2009). The absence of *Leucocytozoon* is therefore most likely linked to an absence of vector species in the area.

It is likely that the presented blood parasites prevalence in the current study are conservative. Microscopic screening is labour intensive and provides somewhat lower estimates of blood parasite prevalence than molecular methods, such as PCR-based detection methods, especially for the smaller intracellular parasites such as *Plasmodium* spp. and *Haemoproteus* spp. (Fallon et al. 2003; Garamszegi 2010; Jarvi et al. 2002). Microscopic screening is also considered to vary considerably depending on the quality of the slides, and the experience of the observer (Campbell & Ellis 2013; Valkiūnas et al. 2008). In addition, birds with heavy infections of blood parasites typical of the primary acute stage of infection, are known to have decreased movement patterns and are less likely to be captured in mist nets (Valkiūnas 1993), thus the prevalence of blood parasites may be underestimated.

4.2 Prevalence and intensity of parasites infections in primary and logged forests

There was no overall difference in ectoparasite prevalence or intensity between forest types (Figure 4). Only the study of Hill (2013) have investigated differences in avian ectoparasite loads between different forest habitats at a community level by dust-ruffling, and the data of that study is incorporated into this study (the 2013 dataset). The 2014 dataset displayed no significant differences in overall ectoparasite load between forest types, while the 2013 dataset showed a significant difference with over twice the mean ectoparasite load in primary forest

compared to logged. The individuals with highest intensity of ectoparasites (a total of 208, 300, 309 and 337 ectoparasites each) were of species that did not have sampled individuals in both forest types, and were subsequently excluded from the analysis. Even without these, the distributions remained highly aggregated, and when analysing the restricted datasets of 2013 and 2014 separately, all of the individuals with highest intensity in 2013 were located in primary forest, while the individuals with highest intensity in 2014 were evenly distributed between primary and logged, something that could be ascribed to chance. This could have caused the great differences in the analysis in ectoparasite infestation intensity between the two datasets. Transmission rate of ectoparasites may rely on the few individual hosts with high infection intensities, as their interaction with other potential hosts may have higher infestation probability compared to the individuals with low infestation intensities. The ecological importance of individuals of extreme infection needs further investigation. The ectoparasitic groups might also differ in their response to logging, and in further studies, the groups should be analysed separately.

The prevalence of blood parasites was slightly lower, but not significantly so, in primary forest compared to logged forest in the YSFMA (12.8% in primary, and 19.2% in logged), contrasting with the predictions of Bonneaud et al. (2009), Chasar et al. (2009), and Laurance et al. (2013), that the prevalence of blood parasites would be higher in primary forest compared to disturbed habitats. It is worth highlighting that the increase in logged forest compared to primary forest is in a magnitude of 50%. This is a substantial increase, and needs further investigation with larger sample sizes and study replications. As identification to specific parasite lineages is very difficult through visual inspection of blood smears, all blood parasites were pooled into genera in this study. This prevents me from investigating if there were differences in the prevalence of the various lineages of parasites between forest types, which Chasar et al. (2009) have demonstrated to vary.

4.3 Species and families

My findings suggest that there is large interspecific variation in parasite prevalence and infestation intensity within the avian community (Figure 5 & Figure 9). This can be caused by three things: 1) The parasite species present may be host specific, 2) there may be species-specific differences in immune responses and susceptibility to infections among host species, or 3) infection may be connected to certain ecological or life history traits of the species. Most

feather mites are considered highly species-specific (Proctor & Owens 2000), and transmission success will be determined by their host species' abundance and intraspecific interaction. Among the blood parasites, *Haemoproteus* are known to be more host-specific than *Plasmodium* (Beadell et al. 2004; Beadell et al. 2009; Zamora-Vilchis et al. 2012). As *Haemoproteus* essentially was the only blood parasite detected in any numbers, it is plausible that the parasite lineages found may be specialists, restricted to only a few host species each or at least to family, corresponding to the findings of Loiseau et al. (2012), with lineages of blood parasites found in rainforest habitats encompassing more specialists compared to more environmentally variable habitats. However, the high diversity of host species found in tropical forests would theoretically encourage less parasite specialisation, as high species diversity and low abundances within host species or vector species restrict the transmission and prevalence of specialist parasites to their appropriate hosts (Hellgren et al. 2009). Generalist parasite lineages can have a higher local prevalence compared to specialist parasites (Hellgren et al. 2009; Pérez-Tris & Bensch 2005), due to the proportion of susceptible hosts in the population and accordingly higher transmission rates. The families were similarly found to differ significantly in parasite infestation intensity and prevalence. This difference could be due to few species being sampled from each family, and could therefore represent a large species bias.

As the sample sizes of each species with a few exceptions were small (N<20), the standard error of the mean are subsequently large and the differences at species-specific level difficult to assess statistically. To acquire a low enough standard error to give a more accurate estimate of the mean intensity of infestation, the sample size of each species have to be increased. Small sample sizes also reduce the accuracy of infection prevalence. The largest problems occur for groups with a prevalence close to 0% and 100%; i.e. in a small group, one is more likely to record low prevalence as absence and high prevalence as complete infection, creating full separation of the results. However, the uncertainty is not a linear relationship, and decreases rapidly as sample sizes increases to 10-20 individuals. Jovani and Tella (2006) argue that a sample size of approximately 15 could be considered acceptable. Only 8 of the species sampled for blood parasites in this study had >15 individuals sampled in total, with >5 in each forest type, considered to be the lowest numbers in groups for acceptable results for many statistical tests. The considerable differences in parasite prevalence and infestation intensity found at species and family level illustrate the complexity of the study system, and set a high demand on the sample sizes needed to draw conclusions about general trends.

4.4 Functional and ecological traits

4.4.1 Overall differences between traits

All birds sampled were understorey birds, thus not illustrating the entire spectre of strata utilised by forest birds. Few terrestrial birds and no canopy species were sampled. In addition, several bird groups were not well represented; e.g. bark gleaners (woodpeckers), carnivores and sallying insectivores. Terrestrial birds have been found to have a higher prevalence of blood parasites than canopy feeding birds (Laurance et al. 2013; Zamora-Vilchis et al. 2012), possibly due to higher contact rates with potential vector arthropods. This cannot be investigated further in my study.

The ectoparasite infestation intensity and prevalence of blood parasites had similar trends across almost all of the functional and ecological traits, with the trait groups with highest ectoparasite loads also having the highest prevalence of blood parasites. The only group that had different responses between ectoparasites and blood parasites were within the primary forest dependence group. Birds preferring primary forest had significantly lower intensity of ectoparasites compared to more generalist birds preferring both forest types and birds preferring logged (secondary) forest. This trend was not found with regards to prevalence of blood parasites, where no statistical significant differences were found between the forest dependency groups. The low level of intensity of ectoparasites in primary forest dependent birds was produced by very low levels within logged forest, which is difficult to explain ecologically. It could, however, be caused by low sample sizes and random fluctuation, as all species included as primary forest dependent birds have naturally more sampled individuals in primary forest than in logged forest.

The ectoparasite loads for nectarivores and insectivores observed in this study contrast with previous findings. Behnke et al. (1995) found low intensity of infestations of feather mites in insectivores, suggesting this might be because of the anatomy of the beak that enable most of them to effectively preen and clean their feathers. Insectivores were here found to harbour medium intensities of ectoparasites. It has also been proposed by Lyra-Neves et al. (2003) that nectarivores and frugivores are more susceptible to infestations by feather mites, which is confirmed for frugivores but not for nectarivores in this study. In contrast, insectivores are associated with higher prevalence of blood parasites compared to frugivores and nectarivores

(Laurance et al. 2013; Ribeiro et al. 2005). However, my findings challenge this, with birds feeding on insects alone having similar low prevalence of blood parasite to nectarivores/insectivores, while birds including fruits in their diet had a significantly higher prevalence.

Birds considered nectarivores/insectivores are usually flowerpeckers, and belong mainly to the family *Nectariniidae*. These had few ectoparasites and a low prevalence of blood parasites. In fact, *Arachnothera longirostra* (LSPHUN) had no infected individuals of blood parasites, despite its high sample size, and only a mean number of 3.6 ± 0.6 SE ectoparasites. In contrast, most of the species considered frugivores/insectivores had a high mean intensity of ectoparasites and medium to high prevalence of blood parasites. They mostly belong to the family *Pycnonotidae* and are mainly foliage gleaners, which accordingly also had high mean intensity of ectoparasites. This difference could be attributed to behaviour leading to lower contact rates with potential vectors. The flowerpecking birds are similar to the hummingbirds of the Neotropics, with small body sizes and a typically rapid movement pattern (Ödeen & Håstad 2010; Zusi 2013). They may thus avoid blood-sucking arthropods. The medium to high levels of both ectoparasites and blood parasites among foliage gleaners (frugivores/insectivores) can possibly be explained by one specific aspect of their behavioural ecology. Foliage gleaners very often participate in mixed-species flocks together with other understorey insectivores with high foraging activity rate. Such flocks are a common phenomenon in tropical forests and one hypothesis link them to predator avoidance (Thiollay 1999). Colonial breeding, group-living birds and birds participating in mixed-species flocks are considered more susceptible to infection by both ectoparasites and blood parasites, due to the high interaction rate between host individuals (Bennett et al. 1978; Poulin 1991; Ribeiro et al. 2005). The tendency to higher sociality and thus a higher interaction rate between foliage gleaners can explain the higher parasite prevalence and infestation intensity in foliage gleaners compared to flowerpeckers (Thiollay 1999).

There was higher prevalence of blood parasites in birds with restricted geographic ranges (endemic) compared to wide-ranging birds (non-endemic). This could be explained by the findings of Loiseau et al. (2012), where avian species with restricted ranges were found to host more generalist blood parasite lineages, while wide-ranging avian species were more prone to infection by specialist parasite lineages. In addition, Laurance et al. (2013) found that birds

preferring rainforest habitats had higher prevalence of blood parasites compared to birds preferring fragments or travelling between both habitats. However, in this study the birds preferring primary forest did not differ from those found equally in primary and logged, or preferring logged forest. This is perhaps due to the exclusion of species only present in one forest type in this study, and the preference of each species is based on a limited dataset.

Increasing bird body size was positively linked with both ectoparasite infestation intensity and blood parasite prevalence. This is consistent with the findings of Rózsa (1997), and Møller and Rózsa (2005) for ectoparasites, and Scheuerlein and Ricklefs (2004) for blood parasites. The higher number of ectoparasites found on larger birds can simply be explained by the larger surface area on which they can occur compared to smaller birds. Larger birds also produce and radiate more carbon dioxide. This attracts blood-sucking arthropods and the larger surface makes them an easier target (Bennett et al. 1978; Poulin 1991; Ribeiro et al. 2005; Thiollay 1999).

4.4.2 Differences between forest types and traits

Few trait groups differed in parasite load and prevalence between forest types. Frugivores/insectivores, and subsequently foliage gleaners, which encompass mainly the same species, had much higher prevalence of blood parasites in logged forest compared to primary forest. Many frugivores and nectarivores are considered opportunistic species and unlikely to be impacted by logging (Johns 1988; Meijaard et al. 2005), and often increase in numbers (Cleary 2002; Cleary et al. 2007; Edwards, F. A. et al. 2013; Lambert 1992), and species richness (Cleary 2002) following logging. They take advantage of the burst of flowers and fruits produced by both pioneer species and the remnant climax trees, as a reaction to the opening of the canopy cover (Lambert 1992). The changes in foraging behaviour may lead to a higher interaction frequency with potential insect vectors, as they forage closer to the ground. The increase in undergrowth by pioneer saplings and lianas following logging, also increase suitable habitats for the invertebrates (Wong 1986). It could also be explained by a participation in mixed-species flocks. The predicted effects of logging on the parasite infestations of mixed-species flocks are, however, ambiguous. Mixed-species flocks are more common in primary forest than in logged forests with overall flocking propensity declining with gap frequency and openness of the forest (Thiollay 1999). This is then leading to the prediction that these birds should have lower levels of parasites in logged forest compared to primary, as their probability

of parasite encounters would decline in logged forest. However, as mixed-species flock species are considered vulnerable to logging (Sodhi et al. 2004b; Thiollay 1997), the increase in prevalence of blood parasites found in this study could be linked to lower immune responses due to stress.

Non-endemic birds had lower levels of ectoparasites in logged forest compared to primary, whereas the endemic birds had a tendency for higher levels of ectoparasites in logged forest compared to primary. The lower levels of ectoparasites on non-endemic birds compared to endemic birds in logged forest could indicate that they do better than the endemic birds in logged forest, which is supported by (Meijaard et al. 2005), who reported that endemic species are inherently vulnerable to logging.

Large bodied avian species are more prone to population declines and have an increased risk of extinction after logging (Castelletta et al. 2000; Cleary et al. 2007; Meijaard et al. 2005; Thiollay 1997). However, this is more often at a regional rather than local scale, as large birds usually roam larger areas (Gaston et al. 1997). Large birds (size class III and IV) had markedly higher prevalence of blood parasites in logged forest compared to primary, while smaller birds (size class I and II) had marginally lower prevalence in logged forest compared to primary (Figure 11). Similar trends were found for the ectoparasites, although not as pronounced (Figure 7). The increase in parasite load and prevalence among larger birds could be linked to environmental stress following logging. However, none of the birds surveyed in this study are of any substantially large size compared to for example hornbills (*Bucerotidae*) and pheasants (*Phasianidae*), which have been the subject of previous studies (Castelletta et al. 2000; Meijaard et al. 2005). It is therefore difficult to assess whether the general relationship between bird size and logging can be explained from the recorded differences in parasite loads and prevalence, or rather by other traits linked to the larger species in this study.

4.5 The correlation between body condition indices and avian parasites

Very few birds exhibited any considerable amounts of tracheal or abdominal fat storage in this study. Fat stores are seen as energy reserves necessary for many important functions, like reproduction or winter survival, but come at a cost of higher predation risk and lower flight agility (Biebach 1996; Witter & Cuthill 1993). There is little literature on pectoral muscle scoring and fat scoring of tropical birds. The body condition indices are primarily used in

research of body condition and fitness of migratory birds and birds of temperate and cold climates with highly seasonal life cycles (Gosler 1996; Labocha & Hayes 2012; Smith & Moore 2003; Witter & Cuthill 1993). This may not be readily transferable to birds from tropical regions, which is defined by a lack of seasonality and most birds are sedentary, especially in Borneo. Fat stores in tropical birds could then possibly be largely a disadvantage, as reduced mobility may reduce fitness considerably. Ward (1969) found low fat levels with little seasonal variation for sedentary birds in tropical Southeast Asia, proposing that birds of predictable, non-fluctuating environments may not need to have fat reserves. This corresponds well to this study where birds scoring zero on the fat score index were abundant, whereas birds scoring zero is usually considered rare in temperate areas (Labocha & Hayes 2012). However, fat storages are also seen as an indicator of food scarcity or habitat quality (Biebach 1996; Katti & Price 1999). It could in this study highlight whether or not logged forest had different food availability than primary forest. Nutritional or environmental stress is also generally assumed to elevate the pathogenicity of blood parasites (Bennett et al. 1993), and thus decreasing the body condition. Changes in body condition could also possibly be linked to stress caused by parasite prevalence and infestation intensity.

However, the two scores of body condition used in this study, fat score and muscle score, were poor predictors of ectoparasite loads or prevalence of blood parasites. This may be explained by the type of parasites prevalent in the current study. The main ectoparasites and blood parasites were feather mites and *Haemoproteus*, respectively, which both are considered to have low or no pathogenic effect on the birds (Atkinson 1991; Galván et al. 2012). No difference was found in body conditions between the two forest types, suggesting that the ecological predictors of body condition in tropical birds do not differ between primary and logged forest. Fat score and muscle scores did not correlate, while wing length was positively correlated with muscle scores and negatively correlated with fat scores. This indicates that larger birds had more developed pectoral muscles, but less fat storage. However, the correlation tests do not take into account the variation within species and sex. There are obvious variations in wing length among species, within species and between males and females, and avian species are considered to exhibit clear differences in the pectoral muscle morphology (Harper 1999). This is probably true for fat stores as well. The birds sampled exhibited little overall variation in fat and muscle scores. If the birds differ little in the condition index with which it is being correlated, it will be difficult to detect correlations (Labocha & Hayes 2012). The use

of body condition indices explained little in this study. They may not be suitable to investigate differences in avian-parasite dynamics or quality of habitat types for the avian community in tropical regions, and would be difficult to link to immune responses. Other measurements of body condition, like body weight, is necessary to further investigate the appropriateness of using fat and muscle score indices for assessment of body condition of tropical birds.

4.6 Correlation between ectoparasites and blood parasites

There was a visible connection between intensity level of ectoparasites and prevalence of blood parasites in species, families and trait groups, with those having highest infection intensity of ectoparasites also having the highest prevalence of blood parasites, like *Tricholestes criniger* (HBBUL) and *Trichastoma bicolor* (FBAB). This indicates that the susceptibility to both ectoparasites and blood parasites are connected. Tested on an individual level, birds infected with blood parasites had higher intensity of ectoparasites compared to birds not infected with blood parasites. Higher prevalence of ectoparasites was also linked to birds found infected with blood parasites, although this correlation was only approaching statistical significance. This indicates that birds already infected with blood parasites may be more susceptible to infestations of ectoparasites, or *vice versa*.

Multiple infections of blood parasites are considered more harmful to birds than the accumulated effect of individual infestations (Davidar et al. 2006; Marzal et al. 2008). There appears to be no literature on the potential accumulating costs of being infested by both blood parasites and ectoparasites, but one can assume that the overall effect of combined endo- and ectoparasite infections could be similar to that of multiple blood infections. However, the difference in ectoparasite infestation intensity and prevalence between birds that tested positive or negative for blood parasites was small, and the low pathogenicity of the major parasitic groups would predict little decline in immune responses due to multiple infections.

4.7 Other important variables in the host-parasite dynamics

Changes in the prevalence of blood parasites are potentially more dependent on alterations in abundance and species composition of the vector species, than their host species (Bonneaud et al. 2009; Chasar et al. 2009). Areas in or at the edges of heavily altered logged forest sites will experience higher desiccation and increased levels of sunlight reaching the substrate. This

could subsequently lead to decreased densities of arthropod species that prefer shaded water bodies as their breeding sites. However, little is known about the population changes of avian blood parasite vectors following logging. Anopheline mosquitoes, responsible for transmitting human malaria (*Plasmodium sp.*), are found to have complex species-dependent reactions to deforestation and forest degradation, but overall appear to increase in degraded habitats, thus increasing the prevalence of malaria (Vittor et al. 2006; Vittor et al. 2009). This contrasts with results for the prevalence of avian *Plasmodium* and *Haemproteus* (Bonneaud et al. 2009; Chasar et al. 2009). Further investigation into their biology and the interaction between vector and host, would be necessary to predict more accurately how the avian-parasite dynamics with regards blood parasites may be affected by logging.

5. Conclusions

I will here answer the questions asked earlier, followed by suggestions for further research. Firstly, is body condition of host species correlated to parasite infestation intensity or prevalence? No link was found between parasites and body condition of their hosts, indicating that the avian parasites present in this particular avian community have little or no detrimental effect on the body condition of the hosts. However, they may not be suitable indicators of any unbalance in the avian community produced by an alteration of avian-parasite dynamics. Body condition indices have been little used on tropical birds prior to this study, and the transfer value from temperate ecosystems needs to be further investigated. Secondly, are ecological and functional traits of the host species associated with infection intensities or prevalence? The evident variation between the different ecological and functional traits, and their complex reactions to logging, highlights the importance of detailed ecological knowledge of the study system. The inherent tolerance levels of parasite infections are considered species-specific, and may be linked to avian groups vulnerable to alterations in environmental conditions. Investigating these traits in more detail could reveal more ecological explanations of the differences in parasite infestation intensity and prevalence in the Bornean forests. Thirdly, are infestations of ectoparasites and blood parasites related? Interestingly, prevalence of blood parasites and infestation intensity and prevalence of ectoparasites seem interconnected, within species, families and trait groups, and on an individual basis. Birds already infected with blood parasites were found to have significantly higher intensity of ectoparasites compared to birds not infected with blood parasites. This suggests that an initial parasite infection may negatively affect the immune responses, thus increasing the susceptibility to other infections. The effect of multiple infections of ectoparasites and blood parasites combined is little studied, and needs further investigation. Finally, does parasite infestation intensity or prevalence differ between primary and logged forest? Parasite loads and prevalence did not differ significantly between forest types. This suggests that these two habitats are very similar concerning the ecological factors behind parasite prevalence and infestation intensity. However, blood parasites had a 50% increase in prevalence from primary to logged forest, although not significant. This possible increase contradicts the findings of other studies, and ought to be further explored. The overall results between forest types were likely confounded by large interspecific and trait-specific variation, which may be equally or more important to the ecological functioning of the forest than what the overall parasite presence could indicate. That only a few significant forest type interactions were found is likely an effect of the limited sample sizes within species

groups, and the large variance constructed by highly aggregated distributions of parasites. Low sample sizes prohibited a thorough species-specific analysis of parasite intensity and prevalence between primary and logged forest, and would need to be increased in future studies. Further advances to this field of research will benefit strongly from a combination of detailed and taxonomically defined studies. For example, process-based studies aimed at elucidating the physiological and mechanistic limitations to parasite transfer and survival, and large-scale meta-analysis, combining and comparing effect sizes from several related studies, thus overcoming the limitations of small sample sizes.

The changes in intensity and prevalence of avian parasites and the implications for the avian community following logging remain difficult to predict, as host-parasite systems are complex and subject to many uncontrolled variables. There is existing evidence that selectively logged forest in Southeast Asia is of similar quality as primary forest for biodiversity conservation purposes (Berry et al. 2010; Edwards et al. 2011; Edwards, D. P. et al. 2013). This also seem the case for the bird-parasite dynamics of the forest-dwelling avian community. Logging did not lead to any detectable deterioration of avian health when considering body condition or avian parasites, but uncertainties connected with the results suggests that more investigation is needed. The contrasts between still forested land, however degraded, and deforested land are considerable, when considering both abiotic and biotic factors. The effect on avian-parasite dynamics will by all prognoses be much higher in deforested and heavily fragmented habitats than in logged forests (Brearley et al. 2013; Daszak et al. 2000; Harvell et al. 2009; Lafferty & Holt 2003; Sehgal 2010). More information about the alteration of avian-parasite dynamics in deforested areas is required to enable comparisons between all three habitats. Areas of primary forests remain crucial to the survival of many species, but this study underlines the importance of implementing solid conservation schemes for logged and degraded forests in Southeast Asia, to conserve buffer habitats for forest-dwelling birds.

6. References

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