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Intestinal parasite communities of six sympatric lemur species at Kirindy Forest, Madagascar

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Abstract. Intestinal parasites impact host health, survival and reproductive success and therefore exert selective pressures on hosts' ecology and behavior. Thus, characterizing and comparing the parasitic fauna of different wildlife hosts sharing the same habitat can provide insights into the mechanisms underlying variation in parasitism, as well as the role of parasites as possible conservation threats. Several host traits have been proposed to generate differences in parasite diversity among different host species, including phylogeny, host body mass, host longevity, diet, and differences in ranging and social behavior. Here, we provide an overview of intestinal helminths and protozoa detected by fecal microscopy in six sympatric lemur species in Kirindy Forest, western Madagascar. The described patterns indicate that host phylogeny and diet may play an important role in shaping intestinal parasite assemblages in this system, as the closely related, omnivorous cheirogaleids showed the strongest overlap in parasite communities. No indication was found for an effect of body mass or longevity on parasite species richness. Regarding the effect of sociality, the two group-living lemur species, *Propithecus verreauxi* and *Eulemur rufifrons*, harbored directly transmitted parasites at higher prevalence than solitary foragers, but not at higher diversity. Effects of season and sex on parasite prevalence confirm the results of previous studies, with higher prevalence in the energetically demanding dry season and a male bias in parasitism. We highlight the opportunities of exploring the parasitic fauna of wildlife from a community ecology and evolutionary perspective, and identify prospects for future research on lemur parasitism.

1 Introduction

Parasites affect host survival and reproduction and thus constitute an important selective force shaping host physiology, ecology and behavior (Coltman et al., 1999; Nunn and Altizer, 2006; Wood and Johnson, 2015). Specifically, intestinal helminths and protozoa may cause reduced energy uptake, pathological damage and decrease their hosts' reproductive success (Hudson et al., 1992, 1998; Delahay et al., 1995; Hillegass et al., 2010). In addition, they impact the host's immune system and alter gut microbial communities (Kreisinger et al., 2015; Reynolds et al., 2015), potentially increasing host susceptibility to bacteria or viruses (Cox, 2001; Ezenwa and Jolles, 2015).

Thus, natural selection should favor mechanisms that reduce exploitation by parasites, whereas parasites evolve mechanisms to circumvent these defense strategies and to secure their ecological niches in this evolutionary arms race. As a consequence, considerable differences in parasite species richness may be generated between different host species. Understanding the factors contributing to this variation in parasite diversity is relevant for fundamental questions in ecology (Poulin, 2004) as well as for species conservation (Kamiya et al., 2014). Host switching, intra-host speciation

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and loss of parasites over evolutionary time are the principal mechanisms involved, which can be influenced by host ecological characteristics like body size, longevity, diet, substrate use and social organization (Poulin, 2004). Furthermore, parasites may co-speciate with their hosts so that common ancestry is an additional important determinant of shared parasite communities between related species (Poulin, 2004). However, empirical support for the role of these factors is mixed and their relative importance is not well understood (Poulin, 2004; Kamiya et al., 2014; Morand, 2015). We therefore first discuss these factors in more detail.

First, because hosts are regarded as insular habitats for their parasites, it has been proposed that larger-bodied hosts provide more ecological niches for parasites and should therefore harbor a richer parasitic fauna (Kuris et al., 1980; Poulin, 1995; Gregory et al., 1996). Evidence for a correlation between host body size and intestinal parasite species richness has, for example, been found in tropical freshwater fish (Guégan et al., 1992) and ungulates (Ezenwa et al., 2006). In several meta-analyses across mammals, however, body mass was only a significant predictor of parasite richness if host phylogeny was not controlled for (Poulin, 2004). Likewise, in a meta-analysis across primates, body mass was only positively correlated with parasite richness in non-phylogenetic models (Vitone et al., 2004). Therefore, it appears that larger bodied mammals do harbor richer parasitic faunas, but this pattern may be explained mainly by inheritance of ancestral parasites through phylogeny (Poulin, 2004).

Second, longer-lived hosts may experience more transmission events throughout their lifetime and are therefore expected to harbor more parasite species (Morand and Harvey, 2000). However, if parasites contribute to host mortality, a negative association between parasite species richness and longevity seems more likely (Cooper et al., 2012). Additionally, longevity is often positively correlated with host body size, making it difficult to distinguish between these two factors (Poulin, 2004). Controlling for host body mass, Morand and Harvey (2000) found a negative correlation between longevity and parasite species richness across mammals. The same pattern was found in ungulates (Ezenwa et al., 2006; Cooper et al., 2012), whereas no association between longevity and parasite species richness was found in carnivores and primates (Cooper et al., 2012). Thus, evidence for a positive association between longevity and parasite species richness is weak and it seems more likely that parasite-induced mortality has selected for short life histories and fast reproduction in some taxa (Cooper et al., 2012).

Third, many helminths with complex life cycles are transmitted via ingestion of intermediate hosts (Guégan and Kennedy, 1993; Vitone et al., 2004). Host diet should therefore have a strong impact on parasite communities. Carnivorous and insectivorous mammals are expected to harbor more indirectly transmitted parasites relative to herbivorous species. In a study across primates, no support for this pattern was found, however (Vitone et al., 2004). Until now, diet as a predictor of parasite richness has been examined in too few comparative studies to allow drawing general conclusions across taxa (Kamiya et al., 2014).

Fourth, ranging behavior can influence exposure to fecal-orally transmitted parasites by mediating contact with feces (Freeland, 1980; Hart, 1990). More intensive ranging should lead to an increased probability of contact with fecally contaminated substrates, and indeed ranging intensity correlates with helminth richness in African ungulates (Ezenwa, 2004) and primates (Nunn and Dokey, 2006). Likewise, in carnivores, rodents and lagomorphs home range size was found to correlate negatively with helminth richness (Bordes et al., 2009), lending support to the fecal exposure hypothesis. In this context, arboreality has also been evoked as a parasite avoidance strategy, limiting contact with infectious parasite stages present in soil (Nunn et al., 2003; Loudon and Sauther, 2013). However, the only comparative study we are aware of that explicitly tested the influence of this behavioral trait on parasite species richness failed to find a significant effect (Nunn et al., 2003). Therefore, this hypothesis needs additional testing in future studies.

Finally, epidemiological theory predicts that transmission of parasites increases with animal density and, thus, represents one of the major disadvantages of gregariousness (Alexander, 1974; Anderson and May, 1982; Anderson et al., 1986; McCallum et al., 2001). Consequently, gregarious hosts should harbor more parasites than solitary species, and species richness should increase with group size. Indeed, an association of gregariousness with parasite diversity has been found in fish (Ranta, 1992), and gregarious African ungulates display both an increase in parasite prevalence and infection intensity as compared to solitary species (Ezenwa, 2004). Furthermore, a significant relationship between host density and parasite species richness has been found across primates (Nunn et al., 2003). However, a meta-analysis including a wide range of host species from mammals to insects revealed that effect sizes of group size on parasite species richness are generally low, except for animals living in large aggregations (Rifkin et al., 2012). In summary, there is overall support for an association between parasite risk and a gregarious lifestyle, but this relationship varies considerably across taxa (Rifkin et al., 2012).

Here, we examine the intestinal parasite communities of six sympatric lemur species in Kirindy Forest, western Madagascar. To our knowledge, this is the first systematic study comparing intestinal parasite communities of more than two sympatric lemur species. Although the number of studies investigating lemur parasitism has recently increased (e.g., Clough, 2010; Rasambainarivo et al., 2013; Larsen et al., 2016), knowledge on the parasitic fauna of these threatened primates still remains comparatively limited. The host species studied here share the same habitat and are thus theoretically exposed to the same set of parasites, but they differ in their degree of phylogenetic relatedness, body mass,

Table 1. Characteristics of six lemur species inhabiting Kirindy Forest, Madagascar.

Species	Family	Body mass	Life span	Diet	Activity pattern	Social organization	References
Microcebus berthae	Cheirogaleidae	22–49 g	unknown, probably similar to *M. murinus*	omnivorous, narrow feeding niche	nocturnal	dispersed groups	Schülke and Ostner (2005), Dammhahn and Kappeler (2008)
Microcebus murinus	Cheirogaleidae	35–110 g	mean 2–3 years, up to 11	omnivorous, broad feeding niche	nocturnal	dispersed groups	Schülke and Ostner (2005), Dammhahn and Kappeler (2008), Hämäläinen et al. (2014)
Cheirogaleus medius	Cheirogaleidae	80–270 g	> 20 years (in captivity)	omnivorous	nocturnal	dispersed pairs	Fietz and Ganzhorn (1999), Schülke and Ostner (2005), Blanco and Zehr (2015)
Mirza coquereli	Cheirogaleidae	270–330 g	up to 17 years (in captivity)	omnivorous, including small vertebrates	nocturnal	solitary	Kappeler (1997), Schülke and Ostner (2005), Fischer and Austad (2011)
Eulemur rufifrons	Lemuridae	2.0–2.3 kg	> 20 years	frugivorous, feeds on animal matter occasionally	cathemeral	group-living	Ganzhorn et al. (1999), Donati et al. (1999), Schnoell and Fichtel (2013)
Propithecus verreauxi	Indriidae	2.4–4.4 kg	> 20 years	strictly foli- and frugivorous	diurnal	group-living	Kappeler and Fichtel (2012)

life histories, diet and social organization, as detailed in Table 1. Thus, variation in patterns of parasitism can be expected based on the hypotheses outlined above.

Four of the species studied (*Microcebus murinus*, *Microcebus berthae*, *Cheirogaleus medius* and *Mirza coquereli*) belong to the family Cheirogaleidae and exhibit a nocturnal lifestyle. Mouse lemurs (*Microcebus* spp.) are the smallest extant primates. Their average life span in the wild is 2–3 years, although some gray mouse lemurs (*M. murinus*) may live for 10 years or more (Hämäläinen et al., 2014). Mouse lemurs usually produce one litter per year (Eberle and Kappeler, 2006). In contrast, fat-tailed dwarf lemurs (*Cheirogaleus medius*), which are true hibernators, are remarkably long-lived, potentially reaching more than 20 years of age (in captivity, Blanco and Zehr, 2015), but often reproduce only every second year (Lahann and Dausmann, 2010). Coquerel's dwarf lemurs (*Mirza coquereli*) can live to an age of 17 years in captivity (Fischer and Austad, 2011) and appear to reproduce annually (Kappeler, 1997).

All four cheirogaleid species are omnivores, consuming fruit, plant exudates and invertebrates in varying proportions; Coquerel's dwarf lemurs additionally prey on small vertebrates (Dammhahn and Kappeler, 2014). All cheirogaleids forage solitarily but show differences in their degree of association with conspecifics. The two mouse lemur species (*Microcebus* spp.) have overlapping home ranges and share sleeping sites with multiple conspecifics, whereas fat-tailed dwarf lemurs live in dispersed pairs but regularly sleep together in the same shelter (Schülke and Ostner, 2005). Only Coquerel's dwarf lemurs can be regarded as truly solitary (Kappeler, 1997).

The other two lemur species examined here, red-fronted lemurs (Lemuridae: *Eulemur rufifrons*) and Verreaux's sifakas (Indriidae: *Propithecus verreauxi*), live in multi-male, multi-female groups with male-biased dispersal (Ostner and Kappeler, 2004; Kappeler and Fichtel, 2012). Both species are relatively long-lived, reaching more than 20 years of age in the wild (Kappeler and Fichtel, 2012). Red-fronted lemurs have a cathemeral circadian rhythm, characterized by irregular bouts of activity both during the day and the night (Donati et al., 1999). They are mainly frugivorous but occasionally consume invertebrates and small vertebrates, such as chameleons (Claudia Fichtel, personal communication, 2013; Schnoell and Fichtel, 2013). Red-fronted lemurs spend a significant amount of time on the ground and regularly drink from waterholes (Donati et al., 1999; Scholz and Kappeler, 2003). As members of the Lemuridae, they have a relatively fast life history for their body mass (Ostner and Kappeler, 2004).

The largest lemurs inhabiting Kirindy Forest, Verreaux's sifakas, are strictly diurnal. They are herbivorous, feeding mainly on leaves, but incorporate flowers and fruit into their diet based on seasonal availability (Norscia et al., 2006). Being vertical clingers and leapers, they rarely descend to the ground and do not drink from waterholes, but rather they rely entirely on the water content of their diet and on dew present on trees (Kappeler and Fichtel, 2012). Sifakas are characterized by a slower life history than members of Lemuridae (Richard et al., 1991).

Here, we report intestinal parasite richness and patterns of prevalence for these six lemur species as determined by fecal microscopy. Regarding animal diet, we expected omnivores to harbor more parasite species which can be transmitted via intermediate hosts than herbivores. We predicted that the two group-living lemur species would harbor more directly transmitted intestinal parasite species than those with a less cohesive social system, due to more opportunities for transmission events. Because Kirindy Forest is subject to pronounced seasonality, we also compared seasonal variation in parasite prevalence for the three species with the largest sample size, controlling for animal sex. We expected prevalence to be higher during the wet season than during the dry season because of better conditions for parasite survival in the environment during these months.

2 Methods

2.1 Study site

Kirindy Forest is located at approximately 44°39′ E, 20°03′ S in the central Menabe region of western Madagascar. It is characterized as dry deciduous forest and subject to pronounced seasonality, with a dry season lasting from April to October and a hot, wet season from November to March (Kappeler and Fichtel, 2012). The study area is part of a field site operated by the German Primate Center (DPZ) since 1993 and is situated within a forestry concession managed by the Centre National de Formation, d'Etudes et de Recherche en Environnement et Foresterie (CNFEREF). Eight lemur species occur in the study area, four of which are classified as endangered (*Microcebus berthae*, *Phaner pallescens*, *Mirza coquereli*, *Propithecus verreauxi*), one as vulnerable (*Lepilemur ruficaudatus*), one as near-threatened (*Eulemur rufifrons*) and only two as least-concern (*Microcebus murinus* and *Cheirogaleus medius*, IUCN Red List of Threatened Species, 2016). As part of an ongoing long-term study (Kappeler and Fichtel, 2012), small, nocturnal lemurs are regularly captured in live traps for the purpose of biomedical sampling and individual marking. In addition, several social groups of red-fronted lemurs and Verreaux's sifakas have been habituated to human observers and individually marked with microchips and unique collars.

All necessary research permits were obtained from the respective Malagasy and German authorities (Ministère des Eaux et Forêts of Madagascar; Commission ad hoc Flore et Faune (CAFF) of Madagascar; Centre National de Formation, d'Etudes et de Recherche en Environnement et Foresterie (CNFEREF); The Federal Agency for Nature Conservation of Germany). Regarding animal welfare, we followed the "Code of Best Practices for Field Primatology" of the International Primatological Society.

2.2 Sampling and sample processing

Fecal samples from six lemur species were collected in Kirindy Forest from 2006 to 2014 by various researchers. Fecal samples from cheirogaleids were taken during animal handling or from traps following capture in Sherman or Tomahawk live traps from 2010 to 2014 (Hämäläinen et al., 2015b; Rakotoniaina et al., 2016). Fecal samples from *Eulemur rufifrons* and *Propithecus verreauxi* were taken during direct observations within 2 min of defecation. All members of eight adjacent study groups of *Propithecus verreauxi* were sampled during 2013 and 2014 (Springer, 2015), whereas data on parasitism of *Eulemur rufifrons* were taken from Clough (2010), who sampled all members of four adjacent groups in the years 2006–2007.

Fecal samples were stored in 10 % formalin until analysis. All fecal samples were processed using a modification of the formalin-ethyl acetate sedimentation technique, as described in Clough (2010). This technique is commonly used to recover helminth eggs from formalin-fixed fecal samples of wild primates (Muehlenbein and Watts, 2010; Pebsworth et al., 2012) and results in the sedimentation of eggs, larvae and protozoa on the bottom of the test tube during centrifugation (Ash and Orihel, 1987). Parasite stages were microscopically identified to genus level, if possible, based on morphological criteria following the key in Irwin and Raharison (2009). Seasonal prevalence was calculated as the number of individuals infected with a certain parasite, based on the microscopic results of all available samples per individual from that season.

2.3 Statistical analyses

To assess seasonal differences in prevalence, we constructed generalized linear mixed models (GLMMs) with binomial error structure and logit link function for the most prevalent parasites (i.e., with total prevalence across years and seasons $> 10\,\%$) of the three study species which were sampled most intensively. Because sex differences in seasonal prevalence patterns have been reported for *M. murinus* before (Hämäläinen et al., 2015b), we included animal sex as a fixed factor. Interactions between sex and season were initially included and retained in final models, if significant. In this case, models testing the effect of season were constructed for each sex separately, which can be found in the Supplement (Table S1). To control for repeated sampling of individuals and possible differences between years, animal identity and study year were included as random effects in all models. Significance of models was assessed by comparison with null models containing only random effects using the R-function ANOVA with method set to "Chisq".

3 Results

Sixteen unique helminth egg morphotypes and three different protozoan morphotypes were detected in lemur fecal samples. A summary of all morphotypes detected per host species is presented in Table 2. To exclude spurious parasites, we only report morphotypes that were present in more than 1 % of samples from a given species. *Microcebus murinus* and *E. rufifrons* harbored the greatest parasite diversity,

Table 2. Parasite morphotypes detected in six lemur species in Kirindy Forest, Madagascar. Morphotypes with a prevalence of more than 20 % are printed in bold. Morphotypes found in less than 1 % of all samples from a given species are not reported.

Host species	Sample size (samples/ individuals)	Phylum	Family	Parasite morphotype	Transmission mode, life cycle characteristic	Reference
Microcebus berthae	61/14	Nematoda	Trichuridae	*Trichuris* sp.	direct, ingestion of eggs	Pechouskova et al. (unpublished data)
			Ascarididae	*Ascaris* sp.	direct, ingestion of eggs	
		Cestoda	Hymenolepididae	*Hymenolepis* sp.	indirect, insect intermediate host	
Microcebus murinus	1349/827	Nematoda	Subuluridae	*Subulura* sp.	indirect, insect intermediate host	Rakotoniaina et al. (2016)
			Trichuridae	*Trichuris* sp.	direct, ingestion of eggs	
			Ascarididae	*Ascaris* sp.	direct, ingestion of eggs	
			n.a.	Strongylida sp.	direct, infectious larvae develop in the environment	
			Oxyuridae	Oxyuridae sp.	direct, ingestion of eggs	
			Oxyuridae	*Lemuricola* sp.	direct, ingestion of eggs	
			Chabertiidae	*Oesophagostomum* sp.	direct, infectious larvae develop in the environment	
		Cestoda	Hymenolepididae	*Hymenolepis* sp.	indirect, insect intermediate host	
		Trematoda	Heterophyidae	*Metagonimus* sp.	indirect, one or more intermediate hosts, first intermediate host typically snail	
			Opisthorchiidae	*Opisthorchis* sp.	indirect, one or more intermediate hosts, first intermediate host typically snail	
		Apicomplexa	n.a.	Coccidia	direct, ingestion of oocysts	
Cheirogaleus medius	155/131	Nematoda	Subuluridae	*Subulura* sp.	indirect, insect intermediate host	Rakotoniaina et al. (2016)
			Trichuridae	*Trichuris* sp.	direct, ingestion of eggs	
			Ascarididae	*Ascaris* sp.	direct, ingestion of eggs	
			n.a.	Strongylida sp.	direct, infectious larvae develop in the environment	
			Oxyuridae	Oxyuridae sp.	direct, ingestion of eggs	
		Cestoda	Hymenolepididae	*Hymenolepis* sp.	indirect, insect intermediate host	
		Trematoda	Heterophyidae	*Metagonimus* sp.	indirect, one or more intermediate hosts, first intermediate host typically snail	
		Apicomplexa	n.a.	Coccidia	direct, ingestion of oocysts	
Mirza coquereli	35/8	Nematoda	Trichuridae	*Trichuris* sp.	direct, ingestion of eggs	Pechouskova et al. (unpublished data)
			Ascarididae	*Ascaris* sp.	direct, ingestion of eggs	
			Subuluridae	*Subulura* sp.	indirect, insect intermediate host	
		Cestoda	Hymenolepididae	*Hymenolepis* sp.	indirect, insect intermediate host	
Propithecus verreauxi	71/41	Nematoda	Trichostrongylidae	Trichostrongylidae sp.*	direct, infectious larvae develop in the environment	Springer (2015)
Eulemur rufifrons	735/29	Nematoda	Oxyuridae	*Lemuricola* sp.	direct, ingestion of eggs	Clough (2010)
			Oxyuridae	*Callistoura* sp. 1	direct, ingestion of eggs	
			Oxyuridae	*Callistoura* sp. 2	direct, ingestion of eggs	
			Trichostrongylidae	Trichostrongylidae sp.	direct, infectious larvae develop in the environment	
			Strongyloididae	*Strongyloididae* sp.	direct, infectious larvae develop in the environment	
			Trichuridae	*Trichuris* sp.	direct, ingestion of eggs	
		Cestoda	Anoplocephalidae	Anoplocephalidae sp.	indirect, mite or insect intermediate host	
		Trematoda	Dicrocoeliidae	Dicrocoeliidae sp.	indirect, one or more intermediate hosts, first intermediate host typically snail	
		Amoebozoa	Entamoebidae	*Entamoeba* sp.	direct, ingestion of cysts	
		Ciliophora	Balantiididae	*Balantidium* sp.	direct, ingestion of cysts	

n.a.: morphotype cannot be identified to the family level; * a single species as confirmed by genetic analyses (Springer, 2015).

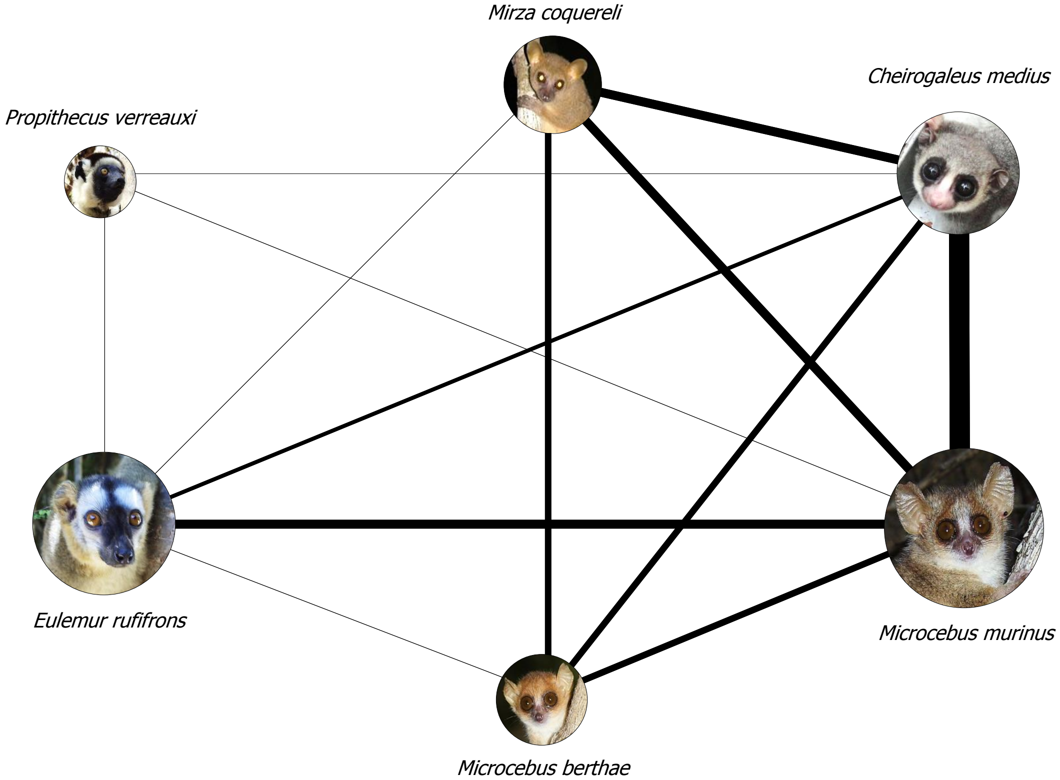

Figure 1. Parasite morphotype sharing network of six sympatric lemur species at Kirindy Forest, Madagascar. Node size corresponds to the number of parasite morphotypes detected in a species, while line width reflects the number of shared morphotypes.

with 11 and 10 distinct morphotypes detected, respectively. However, sample size for *M. berthae* and *M. coquereli* was very low so that we probably have not detected the full parasite diversity infecting these species.

In all four cheirogaleids, the most prevalent parasites were *Hymenolepis* sp. and *Subulura* sp. (transmitted via intermediate hosts) and *Trichuris* sp. and *Ascaris* sp. (directly transmitted nematodes), with the exception that *Subulura* sp. was not found in *M. berthae*. Cheirogaleids also showed the greatest overlap in their parasite communities (Fig. 1). In fact, all parasites that were found in *C. medius*, *M. berthae* or *M. coquereli* also occurred in *M. murinus*. The most prevalent helminths in *Eulemur rufifrons* belonged to the families Oxyuridae and Trichostrongylidae, which have direct life cycles. This was also the only species infected with the directly transmitted protozoan parasites *Entamoeba* sp. and *Balantidium* sp. *Propithecus verreauxi* harbored only one intestinal parasite species, belonging to the family Trichostrongylidae (Springer, 2015).

Seasonal prevalence for *M. murinus*, *C. medius* and *P. verreauxi* from one exemplary study year (2013) is presented in Table 3. Significant seasonal differences in parasite prevalence were detected in *M. murinus* and *C. medius* but not in *P. verreauxi* (Table 4). All parasites that showed significant seasonal variation were more prevalent during the dry, lean season than during the wet season. These included both directly (*Trichuris* sp. and *Ascaris* sp.) and indirectly (*Hymenolepis* sp. and *Subulura* sp.) transmitted parasites.

Sex also influenced prevalence patterns in *M. murinus* and *C. medius*. Male *M. murinus* were significantly more often infected with *Hymenolepis* sp., *Subulura* sp. and *Trichuris* sp. and also showed a stronger seasonal variation in infection rate than females (Table S1). No significant effect of season or sex was found for Strongylida infections in *M. murinus*. Male *C. medius* harbored significantly more *Subulura* sp. and Coccidia sp., but no sex–season interaction was found for this species (Table 4).

4 Discussion

Characterizing and comparing the parasitic fauna of different wildlife hosts sharing the same habitat can provide insights into the mechanisms underlying variation in parasitism, as well as the role of parasites as possible conservation threats. Here, we provide information on the intestinal parasite communities of six of the eight sympatric lemur species which co-occur in Kirindy Forest, Madagascar. These host species represent three lemur families and include the smallest extant primate species, which is endemic to this area.

Table 3. Seasonal prevalence of intestinal parasites for three sympatric lemur species at Kirindy Forest, Madagascar, for the year 2013.

Host species	Total morphotype richness	Parasite morphotype	Prevalence dry season 2013	Prevalence wet season 2013	N (animals sampled) dry/wet
Microcebus murinus	11	*Hymenolepis* sp.	59.50 %	37.36 %	245/182
		Subulura sp.	53.06 %	29.12 %	
		Trichuris sp.	23.67 %	1.10 %	
		Ascaris sp.	20.00 %	1.10 %	
		Strongylida sp.	17.96 %	14.29 %	
		Oxyuridae sp.	7.76 %	1.65 %	
		Metagonimus sp.	2.04 %	0.00 %	
		Lemuricola sp.	0.82 %	0.00 %	
		Opisthorchis sp.	0.41 %	0.00 %	
		Oesophagostomum sp.	0.00 %	0.55 %	
		Coccidia	3.27 %	5.49 %	
Cheirogaleus medius	8	*Subulura* sp.	49.35 %	8.33 %	77/24
		Hymenolepis sp.	48.05 %	4.17 %	
		Trichuris sp.	18.18 %	0.00 %	
		Ascaris sp.	13.00 %	4.17 %	
		Oxyuridae sp.	7.79 %	0.00 %	
		Strongylida sp.	7.79 %	4.17 %	
		Metagonimus sp.	2.60 %	4.17 %	
		Coccidia	2.60 %	8.33 %	
Propithecus verreauxi	1	Trichostrongylidae sp.	97.00 %	89.50 %	33/38

4.1 Patterns of morphotype sharing

We detected a total of 16 different intestinal parasite morphotypes based on fecal microscopy. The most intensively sampled host species, the gray mouse lemur (*M. murinus*), harbored 11 different parasite morphotypes. Eight of these also occurred in fat-tailed dwarf lemurs (*C. medius*). A strong overlap in the parasite communities of *M. murinus* and *C. medius* has been reported before (Schwensow et al., 2010). We show that the most common parasite morphotypes found in these two species, *Trichuris* sp., *Ascaris* sp. and *Hymenolepis* sp., also occur at high prevalence in the two other sympatric cheirogaleids, *M. berthae* and *M. coquereli*. Of these most common parasites of cheirogaleids, only *Trichuris* sp. occurred in the more distantly related *E. rufifrons*, and none in *P. verreauxi*. The fact that overlap in parasite communities was highest within the same host taxonomic family indicates that shared ancestry may be an important factor underlying parasite assemblages in these lemurs.

It has to be kept in mind that sample size was very limited for *M. berthae* and *M. coquereli*, as these species generally occur at low densities and are rarely captured. Thus, we have probably only detected their most prevalent parasite morphotypes, and it is possible that they harbor more parasites at lower prevalence, which they may or may not share with sympatric species. In addition, sample storage may adversely affect egg recovery rates as some morphotypes degrade more quickly in formalin than others (e.g., Lynsdale et al., 2015) so that some infections may have gone unnoticed. However, all samples were stored in formalin and the duration of storage did not differ systematically among host species. Furthermore, we can only report morphotypes here, as species differentiation via genetic analyses was not possible in this study. Thus, whether or not the same morphotypes from different host species actually represent the same parasite species, or just closely related species, remains a subject for future research. At present, species identification based on genotyping is further hampered by the lack of publicly available reference sequences for lemur parasites.

4.2 Influence of ecological and behavioral characteristics on infection patterns

The observed infection patterns indicate that, in addition to phylogeny, host diet may play a role in shaping parasite assemblages in this system. As expected, more indirectly transmitted parasites occurred in the omnivorous cheirogaleids as compared to the two herbivorous species. All cheirogaleids studied here supplement their diet with insects. While the exact life cycles and transmission pathways of lemur parasites are unknown (Irwin and Raharison, 2009), evidence from similar parasites of domestic species suggests that insects serve as intermediate hosts for two of the most prevalent parasites in cheirogaleids, namely *Subulura* sp. and *Hymenolepis* sp. In contrast, strictly herbivorous *P. verreauxi* showed the lowest intestinal parasite diversity, harboring

Table 4. Results of GLMMs testing the influence of sex and season on the most prevalent parasite infections in *M. murinus*, *C. medius* and *P. verreauxi*. Significant P values (< 0.05) are printed in bold.

Host species	N (samples/ individuals)	Parasite	Term	Estimate	Standard error	z value	P value	Null model comparison X^2	Df	P value
Microcebus murinus	1349/827	*Hymenolepis* sp.	Intercept	−0.57	0.19	−2.92	**0.004**	34.18	3	< **0.001**
			Sex (ref. male)	0.47	0.15	3.26	**0.001**			
			Season (ref. wet)	−0.27	0.17	−1.63	0.104			
			Sex × season (wet, male)	−0.68	0.24	−2.77	**0.006**			
		Subulura sp.	Intercept	−0.94	0.37	−2.52	**0.012**	53.56	3	< **0.001**
			Sex (ref. male)	0.83	0.16	5.36	< **0.001**			
			Season (ref. wet)	−0.1	0.18	−0.59	0.553			
			Sex × season (wet, male)	−1.08	0.26	−4.1	< **0.001**			
		Trichuris sp.	Intercept	−2.05	0.41	−4.96	< **0.001**	88.26	3	< **0.001**
			Sex (ref. male)	0.52	0.18	2.92	**0.013**			
			Season (ref. wet)	−1.42	0.33	−4.36	< **0.001**			
			Sex × season (wet, male)	−1.64	0.66	−2.49	**0.013**			
		Ascaris sp.	Intercept	−3.3	0.59	−5.59	< **0.001**	33.93	2	< **0.001**
			Sex (ref. male)	0.15	0.25	0.58	0.562			
			Season (ref. wet)	−1.83	0.36	−5.08	< **0.001**			
		Strongylida sp.	Intercept	−4.19	1.39	−3.01	**0.003**	0.94	2	0.626
			Sex (ref. male)	0.01	0.22	0.06	0.952			
			Season (ref. wet)	−0.21	0.22	−0.95	0.34			
Cheirogaleus medius	155/131	*Hymenolepis* sp.	Intercept	−1.28	0.86	−1.49	0.136	16.57	2	< **0.001**
			Sex (ref. male)	0.3	0.42	0.72	0.474			
			Season (ref. wet)	−2.43	0.79	−3.06	**0.002**			
		Subulura sp.	Intercept	−1.67	0.81	−2.06	**0.039**	19.93	2	< **0.001**
			Sex (ref. male)	0.87	0.41	2.11	**0.035**			
			Season (ref. wet)	−2.29	0.77	−2.94	**0.003**			
		Trichuris sp.	Intercept	−2.11	0.56	−3.74	< **0.001**	8.98	2	**0.011**
			Sex (ref. male)	0.18	0.53	0.35	0.73			
			Season (ref. wet)	−22.07	234.92	−0.09	0.93			
		Coccidia	Intercept	−4.08	1.51	−2.71	**0.007**	10.36	2	**0.006**
			Sex (ref. male)	2.15	0.94	2.28	**0.023**			
			Season (ref. wet)	1.01	1.14	0.89	0.374			
Propithecus verreauxi	71/41	Trichostrongylidae sp.	Intercept	3.66	1.19	3.08	**0.002**	2.68	2	0.262
			Sex (ref. male)	−0.29	0.92	−0.33	0.745			
			Season (ref. wet)	−1.58	1.12	−1.41	0.159			

only one directly transmitted parasite (Trichostrongylidae sp.). Low species diversity of intestinal parasites in *P. verreauxi* has been reported before, also at other study sites in Madagascar (Loudon and Sauther, 2013; Rambeloson et al., 2014).

Only 2 of 10 parasites harbored by the mainly frugivorous *E. rufifrons* are indirectly transmitted (Dicrocoeliidae sp. and Anoplocephalidae sp.), and these occurred at low prevalence compared to directly transmitted parasites (Clough, 2010). Furthermore, the second intermediate hosts of Dicrocoeliidae and Anoplocephalidae are usually arthropods present in the vegetation, e.g., oribatid mites in the case of Anoplocephalidae (Denegri, 1993), which are accidentally ingested by the definitive host, which explains the presence of these indirectly transmitted parasites in herbivorous animals.

We found no indication for host body mass, longevity or social system as a determinant of intestinal parasite richness in this community. Contrary to the hypotheses that parasite richness should increase with host body mass and age, one of the smallest and shortest-lived species, *M. murinus*, harbored the highest diversity of intestinal parasites, while the largest species, *P. verreauxi*, which is also long-lived, harbored the smallest diversity. As detailed above, host phylogeny and diet may be the main drivers of this pattern. In a meta-analysis across primates, body mass was only a significant predictor of parasite richness in models that did not account for host phylogeny, while host life history was not associated with any measure of parasite species richness in primates (Vitone et al., 2004).

While both Vitone et al. (2004) and Nunn et al. (2003) report a positive association between animal density and parasite richness, we found no clear pattern regarding the influence of social system on infection patterns. Contrary to our prediction, cheirogaleids, which live solitarily or in dispersed social systems, did not harbor fewer directly transmitted parasites than the two group-living species in terms of species diversity. However, prevalence of directly transmitted parasites was lower in cheirogaleids than in the two group-living species.

There was a striking difference in intestinal parasite diversity between the two group-living species. As mentioned above, *P. verreauxi* harbored only one intestinal parasite, whereas 10 different morphotypes were found in *E. rufifrons*. While both species live in multi-male, multi-female groups, they show other behavioral differences which may account for this disparity. *Propithecus verreauxi* rarely descend to the ground and do not drink from waterholes, which may limit contact with environmental parasite stages, whereas *E. rufifrons* spend a considerable amount of time on the ground and regularly drink from waterholes. Nonetheless, prevalence of Trichostrongylidae sp. in *P. verreauxi* was around 90 %, and this nematode relies on larval development in the environment to become infectious. Active host-seeking behavior and nictation, i.e., raising of the body in response to olfactory cues, may aid the infectious larvae of this parasite to cling to the hosts' fur during limited ground contact events, and facilitate their spread through the population via direct animal-to-animal contact and grooming (Lee, 2002; MacIntosh et al., 2012; Springer, 2015).

4.3 Influence of season and sex on prevalence

We investigated the influence of season and sex on infection status with the most prevalent parasites in a subset of three species, for which a sufficient sample size was available. We found statistically significant effects of season on infection patterns in *M. murinus* and *C. medius* but not in *P. verreauxi*. Regarding *E. rufifrons*, Clough et al. (2010) found no significant seasonal differences in infection status with the five most prevalent parasites infecting this host.

All parasites that showed a significant seasonal difference in prevalence (*Trichuris* sp. and *Ascaris* sp. in *M. murinus* and *Hymenolepis* sp. and *Subulura* sp. in *C. medius*) were more prevalent during the dry season than during the wet season. This runs contrary to our prediction which was based on the fact that environmental parasite stages usually survive better in moist and warm conditions (e.g., Banks et al., 1990; Besier and Dunsmore, 1993; Ramos et al., 2013). This prediction was supported by higher prevalence of intestinal helminths in the wet as compared to the dry season in chimpanzees (Huffman et al., 1997) and African ungulates (Turner and Getz, 2010), for example. Here, higher prevalence in the dry season may reflect increased host susceptibility to infection rather than increased exposure. The dry season in Kirindy Forest is accompanied by energetically demanding conditions for lemurs due to reduced availability of resources like insects, fruit and leaves, which may reduce body condition (Lewis and Kappeler, 2005; Hämäläinen et al., 2014). In addition, an increase of fecal glucocorticoid metabolites has been found in *M. murinus* in the dry season, reflecting higher levels of stress (Hämäläinen et al., 2015a). Thus, immune function may be impaired in the dry season due to a trade-off in resource allocation with other body functions (Sheldon and Verhulst, 1996; Martin et al., 2008) and/or due to the immunosuppressive effects of chronically elevated glucocorticoid hormones (Webster Marketon and Glaser, 2008; Cohen et al., 2012).

Furthermore, both *M. murinus* and *C. medius* showed a male bias in parasitism, with males generally having a higher prevalence. In addition, *M. murinus* males showed a stronger effect of season on infection rates than females. These results confirm those of Hämäläinen et al. (2015b), who reported consistently higher prevalence of the most common parasites in male *M. murinus* relative to females in the dry season. A male bias in parasitism is common in many mammals and birds and has been attributed to immunosuppressive effects of male sex hormones (Klein, 2004; Hoby et al., 2006) as well as to behavioral differences between males and females (VanderWaal et al., 2013; Hämäläinen et al., 2015b) and differences in body mass (Morand et al., 2004).

4.4 Conclusions and prospects for future research

Here, we have provided an overview of intestinal helminths and protozoa detected by fecal microscopy in six sympatric lemur species, which is a first step towards exploring the parasitic fauna of these animals from a community ecology and evolutionary perspective. The described patterns indicate that host phylogeny and diet may play an important role in shaping intestinal parasite assemblages in this system, whereas no indication was found for an effect of body mass or longevity. Regarding the effect of sociality, group-living lemurs harbored directly transmitted parasites at higher prevalence than solitary foragers but not at higher diversity. Effects of season and sex on parasite prevalence confirm the results of previous studies, with higher prevalence in the energetically demanding dry season and a male bias in parasitism.

Despite these important insights, many gaps in our knowledge still remain, e.g., regarding delimitation of cryptic species with the same egg morphotype, parasite life cycles, pathogenic potential and fitness consequences. While sampling of *M. berthae* and *M. coquereli* needs to be intensified in the future, two lemur species, *Lepilemur ruficaudatus* and *Phaner pallescens*, could not be included in this study at all. These species are nocturnal and, in contrast to the four cheirogaleids, difficult to trap (Schülke and Kappeler, 2003; Zinner et al., 2003). Sampling of fresh feces during direct observations at night is equally challenging. Despite these difficulties, sampling should be attempted, as including these species would add further information with regard to the influence of ecological characteristics on parasite assemblages. For example, like *P. verreauxi*, both species are predominantly folivorous, rarely descend to the ground and lead a rather solitary life in dispersed pairs, which may result in little diversity of intestinal parasites or low prevalence.

Madagascar is considered a hotspot of biodiversity and lemurs are regarded as the most threatened group of mammals globally, due to intense habitat destruction and human encroachment (Schwitzer et al., 2014). However, information on lemur parasites still remains limited despite their potential relevance for lemur conservation. To date, the pathogenic potential of lemur parasites can only be inferred from related, better studied parasites of domestic animals. For many species, the exact life cycles and location of the different parasite stages within the host remain unknown (Irwin and Raharison, 2009). Necropsies of wild lemurs have been conducted only rarely, as animals are rarely found dead, e.g., due to high predation pressure. Nonetheless, there is a need to identify which parasites can be potentially more harmful than others to evaluate their impact on fitness and their conservation relevance.

Studying natural variation in parasitism may also shed light on which lemur species may be most at risk of acquiring introduced parasites. For example, the zoonotic protozoan parasite *Cryptosporidium* sp., which is capable of causing severe pathologies in captive lemurs (Charles-Smith et al., 2010), has been detected in two of four lemur species sampled in a rainforest setting in eastern Madagascar (Rasambainarivo et al., 2013). Among the species found positive was the local mouse lemur species, *Microcebus rufus*, which was also shown to harbor potentially diarrhea-associated viruses and pathogenic enterobacteria in two other studies (Bublitz et al., 2014; Zohdy et al., 2015). Mouse lemurs also harbored the greatest intestinal parasite diversity in our study, indicating that ecological and behavioral characteristics may make members of this genus more likely to pick up introduced diseases than other lemurs.

Despite the remaining gaps in our knowledge, this long-term field study continues to provide the unique opportunity of studying host–parasite relationships in a natural setting. For example, repeated sampling of individuals over their life span allows addressing questions related to immunosenescence and fitness outcomes. Hämäläinen et al. (2015b) were able to show a within-individual decline in parasite infections of aging gray mouse lemurs, for example, indicating acquired immunity by older animals rather than immunosenescence. Finally, comparison of the parasitic faunas of the same species assemblages in multiple study areas, which differ for example in the amount of anthropogenic disturbance, can shed light on the impact of environmental factors on animal health and fitness. This information is crucial to assess the coping capacity of populations in light of increasing habitat disturbance and climate change.

5 Data availability

All raw data have been stored in the data bank of the Behavioral Ecology and Sociobiology Unit of the German Primate Center and are available upon request.

The Supplement related to this article is available online at doi:10.5194/pb-3-51-2016-supplement.

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