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Host-related and environmental factors influence long-term ectoparasite infestation dynamics of mouse lemurs in northwestern Madagascar

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Abstract

Parasite infestations depend on multiple host-related and environmental factors. In the case of ectoparasites, which are exposed to the environment beyond the host, an impact of climate, expressed by seasonal or yearly variations, can be expected. However, long-term dynamics of ectoparasite infestations are rarely studied in nonhuman primates. We investigated the yearly variations in ectoparasite infestations of two small primates, the gray (*Microcebus murinus*) and the golden-brown (*Microcebus ravelobensis*) mouse lemur. For a more comprehensive evaluation, we also analyzed the potential effects of yearly and monthly climatic variation (temperature, rainfall) in addition to habitat, host sex, age, species, and body mass, on ectoparasite infestation. Individuals of both host species were sampled in two study sites within the Ankarafantsika National Park in northwestern Madagascar during several months (March–November) and across 4 years (2010, 2011, 2015, 2016). Our results show significant monthly and yearly variations in the infestation rates of three native ectoparasite taxa (*Haemaphysalis* spp. ticks, *Schoutedenichia microcebi* chigger mites, *Lemurpediculus* spp. sucking lice) and in ectoparasite species richness in both mouse lemur species. In addition, significant impacts of several host-related (species, sex, body mass) and environmental factors (habitat, temperature, rainfall) were found, but

Abbreviations: AIC, Akaike Information Criterion; AICc, corrected Akaike information criterion; deltaic, difference in AIC to the best model; EPSR, ectoparasite species richness; f, female; GLMM, generalized linear mixed model; m, male; max, maximum; min, minimum; n.s., not significant; PC, principal component; PCA, principal component analysis; UV, ultraviolet.

with differences in relevance for the different parasite taxa and partly deviating in their direction. Although some differences could be attributed to either permanent or temporary presence of the parasites on the host or to ecological differences between the host species, the lack of specific knowledge regarding the life cycle and microhabitat requirements of each parasite taxon precludes a complete understanding of the factors that determine their infestation dynamics. This study demonstrates the presence of yearly and monthly dynamics in lemur–parasite interactions in tropical, seasonal, dry deciduous forests in Madagascar, which call out for broad ecological long-term studies focusing both on primate hosts and their parasites.

KEYWORDS

environmental change, host-parasite interactions, long-term parasite dynamics, *Microcebus murinus*, *Microcebus ravelobensis*, seasonality

1 | INTRODUCTION

Variations in the parasite load of nonhuman primates have been studied in various host species in recent decades in the context of assessing primate health, understanding host specificity, parasite diversity, host-parasite coevolution, or the impact of parasites on host fitness and population dynamics (e.g., Altizer et al., 2007; Chapman et al., 2005; Pedersen et al., 2005; Whiteman & Parker, 2005). It is generally accepted that a broad suite of host-related factors and the environment beyond the host can impact parasite infestations.

Among the most widely stated host-related determinants of parasite richness and prevalence are species, sex, age, and body condition (e.g., Clough et al., 2010; Durden et al., 2021; Ishii et al., 2017; Klein et al., 2018). The impact of host species on parasite infections can result from differences in ecology and sociality. For example, high host population density can lead to increased interactions between individuals and thus facilitate the transmission of parasites or pathogens (Stringer & Linklater, 2015). Similarly, the social structure of hosts can play a role, as gregariousness can strongly influence the risk of infection (Patterson & Ruckstuhl, 2013). Conversely, social species executing allogrooming might, in turn, have a lower ectoparasite load (Akinyi et al., 2013). Due to differences in hormone levels influencing immunity or to sex-specific behaviors and ranging patterns, host infection susceptibility might vary between the sexes (Klein, 2004; Rodriguez et al., 2015). For instance, Zohdy et al. (2017) found that brown mouse lemur (*Microcebus rufus*) males had significantly more lice than females, which could be due to an immunosuppressive effect of some hormones, like testosterone, and higher encounter rates of male hosts. Rodriguez et al. (2015) found that *Microcebus griseorufus* males had higher tick infestation prevalences probably due to longer foraging times compared to females. Since older individuals could show immunosenescence (Haberthur et al., 2010; Palacios et al., 2007; Zohdy, 2012), or juveniles could have less developed immune systems (Attanasio et al., 2001; Foerster et al., 1997), age has been argued and shown to impact parasitic infections. In a study on wild Japanese macaques (*Macaca fuscata*), Ishii et al. (2017) found that juvenile hosts harbored more louse eggs than adult macaques. As a consequence of nutritional stress, hosts in poorer body conditions are often more susceptible to infections than individuals in better conditions (Beldomenico & Begon, 2010; Kiene et al., 2020; Wikel, 1982). However, Arneberg (2002) found parasite species richness to be positively related with host body mass, probably linked to higher transmission rates and the establishment of more parasite species in those hosts that have higher movement rates and food intake.

Suggested environmental impacts on parasite infestations are habitat type, condition and disturbance, temperature, humidity, rainfall, and seasonality (e.g., Blersch et al., 2021; Chapman et al., 2006; Gillespie & Chapman, 2008; Kiene et al., 2021). For example, habitat fragmentation as a predictor for habitat integrity was shown to impact parasite ecology and infection dynamics. However, previously documented effects of environmental modification were contradictory, since both, higher (Raharivololona & Ganzhorn, 2009; Schwitzer et al., 2010) and lower levels (Kiene et al., 2020; Renwick & Lambin, 2013) of parasite infections have been found in hosts from fragmented and disturbed ecosystems compared to hosts from pristine habitats. These contradicting results, however, may at least be partly explained by the different parasite types they focused on.

Also, climate and its seasonal variations might impact parasites directly or indirectly via their hosts. However, long-term dynamics of parasite infections have only rarely been studied, and the underlying causes driving these dynamics are still under debate. For example, Blersch et al. (2021) found that in wild vervet monkeys (*Chlorocebus pygerythrus*) dwelling in a semiarid riverine woodland, precipitation negatively affected infections with gastrointestinal nematodes of the genus *Protospirura*, while the maximum daily temperature was positively related to infections with a nematode from the genus *Trichostrongylus*. Rodriguez et al. (2015) found that in three noncontiguous dry forests in southwestern Madagascar, ticks

parasitized gray-brown mouse lemurs (*M. griseorufus*) only during the dry season. Moreover, the development and survival of temporary ectoparasites like ticks and chigger mites can depend on humidity, rainfall, and temperature (Berger et al., 2014; Cumming, 2002; Sasa, 1961; Wall & Shearer, 1997). Finally, even though permanent ectoparasites (e.g., sucking lice) should be better protected against environmental fluctuations by their continuous association with the host, they may still be negatively affected by aridity or high ambient temperatures (Kiene et al., 2020; Moyer et al., 2002; Wall & Shearer, 2001a).

On the island of Madagascar, the man-made transformation of natural habitat and climatic fluctuations are severely impacting the entire flora and fauna (Ingram & Dawson, 2005; Vieilledent et al., 2018). The country is inhabited by many endemic vertebrate species, including a large radiation of lemurs (Mittermeier et al., 2010), which host a broad suite of parasite species (Ehlers et al., 2019; Irwin & Raharison, 2009; Kiene et al., 2020, 2021; Klein et al., 2018; Springer & Kappeler, 2016; Zohdy & Durden, 2016). Changes in the distribution of these parasite communities in connection with climate change have already been predicted for the near future by model calculations (Barrett et al., 2013). Since most lemurs are already threatened due to ongoing deforestation and forest fragmentation (www.redlist.org; Schwitzer et al., 2014), it is more important than ever to understand their long-term interconnectivity within their native ecosystems. The investigation of ectoparasites is challenging because it requires direct host examinations, so most multi-year parasitological studies have focused on infections with gastrointestinal parasites (Petrzelková et al., 2010; Rondón et al., 2017), which can be studied noninvasively using fecal samples. Since ectoparasites might be notably and continuously exposed to the environment beyond their hosts, they are particularly interesting study models with respect to their responses to changing environmental conditions.

In this study, we investigate the yearly variation in ectoparasite infestations for two small primate species, the gray (*Microcebus murinus*) and the golden-brown mouse lemur (*Microcebus ravelobensis*) from two sites of dry deciduous forest within the Ankarafantsika National Park in northwestern Madagascar. These sites differ largely in forest structure, forest composition, soil type, and proximity to surface water and, therefore, can be considered different habitats (Chanu et al., 2012; Rendigs et al., 2003; Sehen et al., 2010). Both host species have been studied in a long-term project focusing on their socioecology and population dynamics (Chanu et al., 2012; Henkel et al., 2019/2020; Radespiel et al., 1998, 2003, 2021; Rakotondravony & Radespiel, 2009; Rendigs et al., 2003; Thorén et al., 2011). *M. murinus* and *M. ravelobensis* live in partial sympatry (i.e., occurring together in some forests but alone in others) in the two study sites, exhibit similar body sizes (ca. 60 g), overlapping diets and seasonal reproductive activity (Radespiel et al., 2021; Thorén et al., 2011; Zimmermann et al., 1998). According to previous studies (Kiene et al., 2020; Klein et al., 2018), seasonality, habitat fragmentation, host sex, body mass, and species seem to be important determinants of host ectoparasite infestations. However, the environmental factors driving parasite seasonality, as well as potential yearly variations in infestation patterns have not yet been investigated. We aim to test these and the potential effects of temperature and rainfall variations on the infestation dynamics of different ectoparasite taxa (temporary and permanent) on these two host species. Furthermore, other general factors that are expected to impact parasite dynamics (e.g., habitat, host species, sex, age, and body mass) will be considered. Over a period of 4 years (2010/2011, 2015/2016), all *Microcebus* that were captured and released between March and November each year were permanently marked, and many of them were repeatedly inspected for ectoparasites. Rainfall and temperature are explored as general predictors for the occurrence and richness of ectoparasites. Since high temperatures and low humidity can lead to desiccation and reduced ectoparasite survival (Berger et al., 2014; Kiene et al., 2020; Moyer et al., 2002; Sasa, 1961; Wall & Shearer, 1997), we predict an increase of ectoparasite infestations in years of lower (monthly) temperatures and in years of more rainfall (total or monthly). Moreover, due to their different ecology and life cycles, we predict that the impact of climatic variables will be higher for temporary parasites, such as ticks or chigger mites, that spend most of their life cycle in the environment, for example, as off-host larvae, nymphs, and adults in the vegetation or on the ground (Sasa, 1961; Wall & Shearer, 1997, 2001b), than for permanent parasites, such as sucking lice, which are more protected from outer influences by the stable microclimate on the body of their host.

2 | METHODS

This study received authorization by the Ministére de l'Environment, des Eaux et Forêts Malgache (Authorization no. N102/10/MEF/SG/DGF/DCB.SAP/SCBSE, N103/10/MEF/SG/DGF/DCB.SAP/SCBSE, 101/11/MEF/SG/DGF/DCB.SAP/SCB, no. 102/11/MEF/SG/DGF/DCB.SA/SCB, no. 063/15/MEEMEF/SG/DGF/DCB.SAP/SCB, and no. 34/16/MEEMEF/SG/DGF/DAPT/SCBT.Re) and by Madagascar National Parks. Animal handling and sampling procedures in Madagascar received ethical approval from the Institutional Animal Care and Use Committee of Arizona State University (Protocol: 10-1077R), followed the code of veterinary ethics and the German Protection of Animals Act, and conformed to the accepted principles of animal welfare in experimental science and the principles defined in the European Convention for the Protection of Vertebrate Animals used for Experimental and Other Scientific Purposes (Directive 2010/63/EU). Fieldwork also followed the American Society of Primatologists Code of Best Practices for Field Primatology, the ethical guidelines for the treatment of primates of the Gesellschaft für Primatologie (GfP), and adhered to the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates. The study also conformed to the legal ethical requirements formulated by the Malagasy authorities.

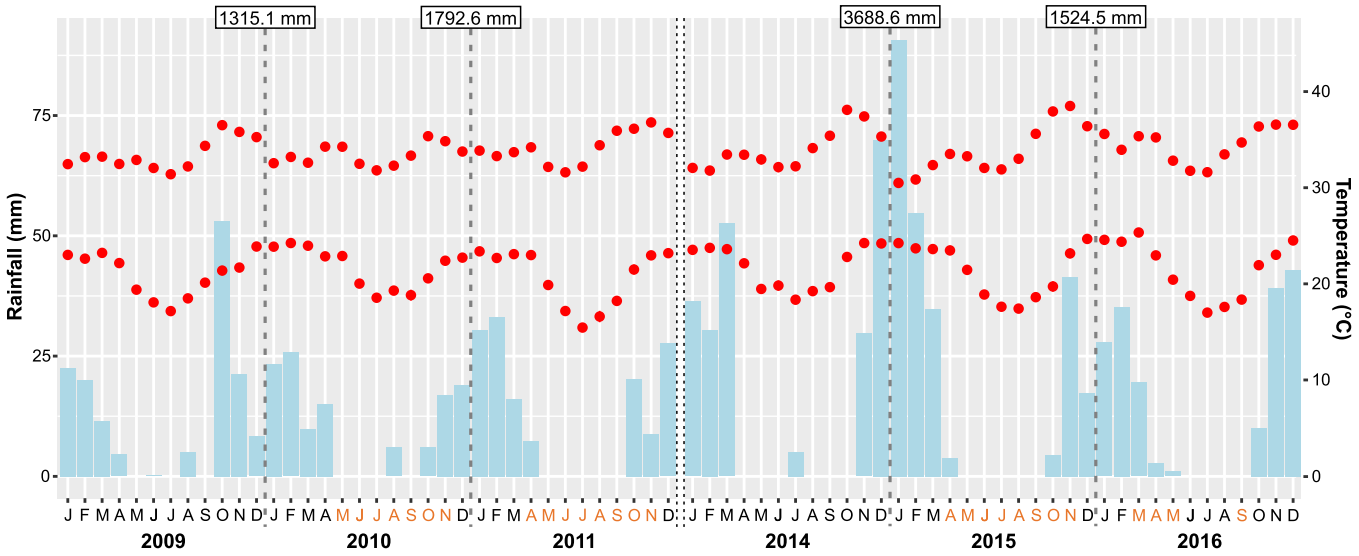

FIGURE 1 Precipitation (mm, monthly sum of daily records, blue bars) and minimum and maximum temperatures (°C, monthly averages of daily records, red dots) per month (January–December) of the four investigated years (2010/2011/2015/2016) and of the year before each sampling period (2009/2014), respectively. Month letters in orange correspond to the sampling periods. Box above: total rainfall (mm) during the respective rainy season (November–April). Climatic data were kindly provided by the Durrell Wildlife Preservation Fund (personal communication, 2017) at the Ampijoroa Forest Station in Ankarafantsika National Park.

2.1 | Sampling period and study sites

Ectoparasite examinations of mouse lemurs were conducted by two main investigators (S. E. K., A. K.) across some months of 4 different years (2010, 2011, 2015, 2016) in the Ankarafantsika National Park in northwestern Madagascar (Supporting Information: Table S1). Data were collected from two separate study sites within the park. The first site, Jardin Botanique A (JBA; 16°19′07.2″ S, 46°48′35.5″ E), is a dry deciduous forest on sandy soil situated near the park headquarters at Ampijoroa at about 190 m elevation above sea level and with no surface water (Chanu et al., 2012). The second site, Jardin Botanique B (JBB, 16°18′02.6″ S, 46°48′44.7″ E), is a section of a gallery forest next to Lake Ravelobe at 89 m above sea level and is partly flooded during the rainy season (Rendigs et al., 2003; Sehen et al., 2010).

The climate in this region is strongly seasonal with a cool dry season from May to October and a hot rainy season from November to April (Figure 1). Ectoparasite sampling covered 3 months of the rainy season (March, April, and November) and all months of the dry season (May–October) (Supporting Information: Table S1). Between 126 and 219 individual mouse lemurs were examined per year, and both sexes were represented in both sites and both species (Table 1).

TABLE 1 Number of mouse lemur individuals examined per year in JBA and JBB in Ampijoroa, Madagascar.

			2010	2011	2015	2016	Total
JBA	Mur.	F	19	19	25	23	86
		M	46	50	31	25	152
	Rav.	F	33	26	47	30	136
		M	53	41	38	353	167
JBB	Mur.	F	0	0	3	4	7
		M	0	0	2	1	3
	Rav.	F	39	28	30	5	102
		M	29	27	19	3	78
Total			219	191 (79)	195 (3)	126 (51)	731

Abbreviations: f, females; in brackets, number of individuals also examined in previous years; JBA, Jardin Botanique A; JBB, Jardin Botanique B; m, males; Mur., *Microcebus murinus*; Rav., *Microcebus ravelobensis*.

2.2 | Host capture and ectoparasite assessment

Mouse lemurs were captured and marked permanently with subcutaneous transponders following standard procedures (Rendigs et al., 2003). Ectoparasite inspections also followed published procedures (2010–2011: Durden et al., 2021; 2015–2016: Klein et al., 2018). The procedures were very similar across years and included systematically inspecting the lemur with particular attention to the head, ears, and thighs, and opportunistic collections of parasites noticed elsewhere during handling. In total, 186 (119 males, 67 females) *M. murinus* and 249 (140 males, 109 females) *M. ravelobensis* were inspected for ectoparasites in JBA, and 9 (3 males, 6 females) *M. murinus* and 154 (66 males, 88 females) *M. ravelobensis* were inspected in JBB. Overall, 67% of the individuals (401/598) were sampled more than once (mean inspections per individual = 3.75 ± 0.17 (standard deviation [SD]); median = 2; minimum = 1; maximum = 45) leading to a total of 2241 examinations

(=ectoparasite inspection events) (Supporting Information: Table S1). For the statistical analyses of host and temporal effects, consecutive ectoparasite examinations of a host individual in intervals of less than 7 days were merged using the following procedure: if there was one or more parasite detections in 7 days, then the lemur was recorded as positive for that ectoparasite, but if all were negative, then it was recorded as absent. In addition, inspection results with lacking body mass values were excluded. With this approach, the final number of sampling events used for modeling was 1940 ectoparasite inspection events stemming from 598 individuals. The term "infestation rate" is used whenever referring to a relative number of inspection events in which a specific ectoparasite type was found. By contrast, the term "prevalence" is used when reporting the proportion of infected individual hosts. For the analysis of the impact of climatic factors under given analytical constraints (see below), ectoparasite inspections with missing climatic values were excluded, and the data set was randomly reduced to one sample per individual with the condition to represent all months as evenly as possible, resulting in a total of 583 individual sampling events.

The presence or absence of the various ectoparasite types was recorded macroscopically in the field, and a small sample of all detected ectoparasite types was taken and stored in 90%–96% ethanol for each host individual and sampling day separately. Collected ectoparasite samples were identified morphologically by applying standard identification methods under light microscopy to verify the field records (Durden et al., 2021; Kiene et al., 2020; Klein et al., 2018; Stekolnikov, 2018; Walker et al., 2003). Presence or absence was recorded for all ectoparasite taxa based on the composite record of field notes and microscopy for each mouse lemur examination. Positive field records for ectoparasites without a collected sample were considered only for ticks, because they cannot be easily overlooked or misidentified. If no field sample was available for other ectoparasite types (e.g., sucking lice, mites), positive records from the field were excluded (=not available) as their difficult macroscopic identification in the field could have led to false positive results.

2.3 | Data analysis

Statistical analyses were conducted for the three most frequent ectoparasites: *Haemaphysalis* spp. (ticks), *Schoutedenichia microcebi* (chiggers), and *Lemurpediculus* spp. (sucking lice), since presence–absence data for other taxa recorded were too sparse for systematic analyses. The presence–absence data for these three parasite taxa per capture event of each individual host and the number of simultaneously present ectoparasite taxa (ectoparasite species richness [EPSR]) were analyzed as dependent variables by fitting generalized linear mixed models (GLMMs) to the sample of 1940 examination records. To investigate host effects and temporal variations, sampling year (2010, 2011, 2015, 2016), sampling month (March–November), a variable combining sampling site and host species (*M. murinus*—JBA, *M. murinus*—JBB, *M. ravelobensis*—JBA and *M. ravelobensis*—JBB), host sex (male, female), host age (juvenile, adult), and host body mass (in gram) were used as fixed variables. As *M. murinus* was not found in JBB across all years and months, the variable combining sampling site and host species was necessary to avoid modeling errors. Juvenile age was deduced from a low initial body mass (clearly below average) and its steady increase over the first months of capture (Radespiel et al., 2021). To control for pseudoreplication based on multiple sampling of single hosts, host identity ("animal ID") was added as a random factor. Since not all months were sampled in all years (Supporting Information: Table S1), two different global temporal models, one with month (global model A) and one with year (global model B) as a fixed factor, were generated for each ectoparasite taxon and for EPSR (Table 2). Since the *p* values for the post hoc comparisons between months in the global model A for ticks were unreliable due to a lack of convergence, the model was simplified (model A.2) using only those factors found to be significant in the global model A. In case of the other dependent variables, simplifying their first global model (A) did not change the results.

A total of 33 climatic variables were available and included in the analyses of the impact of climatic variation on ectoparasite infestation: monthly minimum, monthly maximum, and monthly average temperature, and rainfall amount in the sampling month and in the month previous to sampling (=8 variables); total rainfall during the previous rainy season (=1 variable); and finally monthly rainfall, minimum, maximum, and average temperatures of the previous rainy season (November–April) (=24 variables). Examinations from animals captured during the rainy season (March–April) were excluded from the analysis of the climatic effects (remaining $N = 583$ individuals), since March and April temperatures and precipitations had not yet taken place at that point and the principal component analysis (PCA) would not allow for lacking entries. Due to multiple correlations within the climatic data set, the variables were

TABLE 2 Composition of general global models fitted for each ectoparasite taxon and the EPSR as dependent variables.

	Model used	Data set	Fixed factors	Random factors
Model A	GLMM	1940 sampling events	Month + site_sp + sex + age + body mass	Host individual
Model B	GLMM	1940 sampling events	Year + site_sp + sex + age + body mass	Host individual
Model C	GLMM	583 sampling events	PC1 + PC2 + PC3 + PC4 + PC5	Month

Abbreviations: EPSR, Ectoparasite Species Richness; GLMM, generalized linear mixed model; PC, principal component; site_sp, factor combining sampling site and host species.

first subjected to a PCA that was based on a correlation matrix for all explanatory variables (after standardization of each entry as deviation from the mean, divided by SD). A total of nine uncorrelated principal components (PCs) resulted from the PCA, five of which, with an eigenvalue of >1, were selected for further analyses and explained 96.6% of the variance in the climatic data set (Supporting Information: Table S3). The factor coordinates of cases were used for the subsequent modeling steps and high factor loadings (>0.7 or <−0.7) of climatic variables were used for interpretation (Supporting Information: Table S4). The PCA was performed with STATISTICA 12 (Statsoft Inc.). The same four dependent variables as before (presence/absence of *Haemaphysalis* spp., *S. microcebi*, *Lemurpediculus* spp., EPSR) were analyzed by fitting GLMMs, with the first five PCs from the PCA used as fixed factors with the data set containing one entry per individual ($N = 583$). Preliminary models that contained more than one entry per individual and individual identity as an additional random factor did not converge and were therefore discarded. To distinguish between monthly variations due to seasonal ectoparasite dynamics and the effect of yearly climatic changes, month was added as a random factor.

All models were fitted with binomial assumption and logit-link for the presence–absence data, and Poisson assumption and with log-link for the EPSR. All calculations were done in Rstudio version 4.0.3 (Integrated Development for R. Rstudio Inc., http://www.rstudio.com). Models were fitted using the package "lme4" (Bates et al., 2015). The selection of GLMMs for final interpretation was done for all global models using the automated model selection function *dredge()* of the R package "MuMIn" (Barton, 2020), based on the Akaike Information Criterion (AIC) method (Burnham & Anderson, 2002). The corrected AIC values (AICc) of models with all possible combinations of fixed factors were compared and all best models ($\Delta AIC < 2$) were identified. When the factors year, month and site-species were significant in the best models, pairwise differences between levels were tested with a Tukey test (post hoc analysis), applying the R package "multcomp" (Hothorn et al., 2008). Graphics were obtained using the R package "ggplot2" (Wickham, 2016).

3 | RESULTS

3.1 | Parasite identification and general infestation rates

The investigated hosts were infested by ticks (Acari, Ixodidae), sucking lice (Insecta, Anoplura), and mites of the families Trombiculidae, Laelapidae, and Atopomelidae (Supporting Information: Figure S1). Based on morphology, all ticks were identified as *Haemaphysalis* spp. According to Durden et al. (2018) sucking lice of *M. murinus* were assigned to *L. madagascariensis*, whereas the lice of *M. ravelobensis* belong to the newly described species *Lemurpediculus zimmermanni* (Springer et al., 2023). Trombiculid mites from *M. murinus* were recently described as *S. microcebi* by Stekolnikov et al. (2019) and those of *M. ravelobensis* can also be assigned to this taxon based on the molecular results of Kiene et al. (2020). Morphological species identification for the other two taxa (Laelapidae, Atopomelidae) was, however, only possible to the family level.

Prevalence (=proportion of infested individuals) for Atopomelidae and Laelapidae was generally low, 8% and 5%, respectively (Supporting Information: Table S2). In contrast, 54% and 55% of the individuals were infected during at least one examination with *Haemaphysalis* spp. and *Lemurpediculus* spp., respectively, while we detected *S. microcebi* on 24% of the individuals. Overall, 80% of the 598 individuals carried at least one ectoparasite type at some time point during the study. Overall ectoparasite infestation rates (% of all 2241 examinations) varied between 2% (Laelapidae) to 35% (*Lemurpediculus* spp.). Sixty-three percent of all samples contained at least one ectoparasite taxon (Table 3). Mean EPSR was 0.86 ± 0.03. The infestation rates of laelapid and atopomelid infestations remained at 5% or below in all cases except for Atopomelidae in 2011, when it reached 12% (Table 3).

The sources of variation in ectoparasite infestation were modeled in more detail for the three most frequent parasite taxa (*Haemaphysalis* spp., *S. microcebi*, *Lemurpediculus* spp.) and the EPSR (see below, results for best global models are summarized in Tables 4 and 5). Detailed information for all model results is provided in the Supporting Information: Tables S5–S12.

3.2 | Impact of sampling site and host-related factors (species, sex, age, and body mass)

A significant effect of sampling site and host species was found for two of three parasite taxa and for EPSR (Table 4). Only *Haemaphysalis* spp. did not show any effect of the variable site-species (Supporting Information: Table S5: global model A, p = n.s.). Infestation rates of *S. microcebi* were higher in *M. ravelobensis* inhabiting JBB than in those from JBA and higher than in *M. murinus* from JBA (Supporting Information: Table S6: global model B; $p < 0.0001$). *Lemurpediculus* spp. infestation rates were higher in *M. ravelobensis* from both sites than for *M. murinus* in JBA (Supporting Information: Table S7: both global models; $p < 0.001$). In addition, infestation rates of *M. ravelobensis* were higher in JBA than in JBB (Supporting Information: Table S7: both global models, $p < 0.001$). The EPSR was significantly higher in *M. ravelobensis* from both JBA and JBB compared to *M. murinus* from JBA (Supporting Information: Table S8: both global models; $p \leq 0.002$) but did not differ intraspecifically between JBA and JBB (Supporting Information: Table S8: both global models; p = n.s).

GLMMs revealed significant differences of infestation rates between the sexes for *Haemaphysalis* spp. (Supporting Information: Table S5: both global models, $p \leq 0.001$) and *Lemurpediculus* spp. (Supporting Information: Table S7: global model B, $p < 0.0005$). In both parasite taxa, male hosts were significantly more likely to be infested than females. Consequently, the EPSR was also significantly higher in male hosts compared to females (Supporting Information: Table S8: both global models, $p < 0.0005$). Infestation risk for *S.*

TABLE 3 Occurrence of all detected ectoparasite taxa (relative and absolute numbers) and EPSR (mean ± standard deviation) in the overall sample and separated by host sex, species, age, site, and year.

		Sex		Species		Age		Site		Year			
	Total	Male	Female	*Microcebus murinus*	*Microcebus ravelobensis*	Adult	Juvenile	JBA	JBB	2010	2011	2015	2016
Overall infestation rates	63% (1409/2241)	68% (786/1152)	57% (623/1089)	52% (438/837)	69% (971/1404)	63% (1144/1816)	62% (264/425)	61% (1079/1763)	69% (330/478)	66% (366/555)	73% (360/493)	53% (447/846)	68% (236/347)
Haemaphysalis spp.	28% (637/2241)	34% (391/1152)	22% (246/1089)	29% (240/837)	28% (397/1404)	30% (536/1816)	24% (101/425)	27% (478/1763)	33% (159/478)	40% (225/555)	47% (233/493)	17% (147/846)	9% (32/347)
Lemurpediculus spp.	35% (784/2241)	37% (426/1152)	33% (357/1089)	19% (158/837)	45% (625/1404)	35% (631/1816)	36% (152/425)	36% (637/1763)	30% (146/478)	31% (174/555)	21% (105/493)	37% (309/846)	56% (196/347)
Schoutedenichia microcebi	11% (256/2241)	12% (134/1152)	11% (122/1089)	9% (77/837)	13% (179/1404)	12% (210/1816)	11% (46/425)	8% (145/1763)	23% (111/478)	5% (30/555)	27% (131/493)	7% (55/846)	11% (40/347)
Laelapidae	2% (43/2241)	3% (34/1152)	1% (9/1089)	5% (38/837)	0 (5/1404)	2% (34/1816)	2% (9/425)	2% (41/1763)	0 (2/478)	0 (2/555)	2% (9/493)	2% (17/846)	4% (15/347)
Atopomelidae	3% (63/2241)	4% (44/1152)	2% (19/1089)	5% (40/837)	2% (23/1404)	3% (58/1816)	1% (5/425)	3% (50/1763)	3% (13/478)	0 (0/555)	12% (60/493)	0 (2/846)	0 (1/347)
EPSR	0.86 ± 0.03	0.94 ± 0.04	0.76 ± 0.04	0.68 ± 0.05	0.95 ± 0.04	0.85 ± 0.03	0.90 ± 0.07	0.84 ± 0.03	0.93 ± 0.06	0.79 ± 0.05	1.02 ± 0.07	0.72 ± 0.05	0.95 ± 0.06

Abbreviations: EPSR, Ectoparasite Species Richness; JBA, Jardin Botanique A; JBB, Jardin Botanique B.

TABLE 4 Results of GLMMs with lowest AICc testing the impact of host-related factors and month (model A) or year (model B) on *Haemaphysalis* spp., *Lemurpediculus* spp., and *Schoutedenichia microcebi* infection risk and EPSR.

			Factors					
Dependent variable	Model	AICc	Site- species	Sex	Age	Body mass	Month	Year
Haemaphysalis spp.	A	2121.1	n.s.	Males > Females		+	Jul, Aug, Sep > Apr, May, Jun, Oct, Nov[a]; Oct > Apr, May[a]; Jun > May[a]	
	B	2260.7		Males > Females				2010, 2011 > 2015, 2016
Schoutedenichia microcebi	A	1116.2			n.s.	+	May, Jun, Jul, Aug > Mar, Apr, Sep, Oct, Nov	
	B	1169.3	M. rav JBB > M. mur JBA, M. rav JBA					2011 > 2016 > 2015, 2010
Lemurpediculus spp.	A	1979.2	M. rav JBA > M. rav JBB > M. mur JBA; M. rav JBA > M. mur JBB			−	Oct > Apr, May, Jun, Jul, Aug, Sep; Sep, Nov > May, Jun, Jul, Aug; Mar, Apr, Aug > Jun, Jul; May > Jun	
	B	2252.1	M. rav JBA > M. rav JBB > M. mur JBA; M. rav JBA > M. mur JBB	Males > Females		n.s.		2016 > 2015, 2010 > 2011
EPSR	A	4277.5	M. rav JBA, M. rav JBB > M. mur JBA	Males > Females		n.s.	Aug, Sep, Oct > Apr, May, Jun; Jul > May	
	B	4294.8	M. rav JBA, M. rav JBB > M. mur JBA	Males > Females				2011 > 2016 > 2015, 2010

Abbreviations: −, significant negative effect; +, significant positive effect; AICc, corrected Akaike Information Criterion; dark gray empty field, factor not tested in the model; EPSR, Ectoparasite Species Richness; GLMM, generalized linear mixed model; light gray empty field, factor not included in the best model; M. mur, *Microcebus murinus*; M. rav, *Microcebus ravelobensis*; n.s., not significant.

[a]Result of post hoc comparisons from model A.2.

TABLE 5 Summary of the results of GLMMs with lowest AICc testing the impact of five principal components (PC1–5) derived from all 33 climatic variables on *Haemaphysalis spp.*, *Lemurpediculus* spp., and *Schoutedenichia microcebi* infection risk and on EPSR.

		Principal components				
Dependent variable	AICc	PC1 (rainfall Dec–Mar, overall rainfall, warm Nov, cool Jan–Feb)	PC2 (rainfall Apr, cool Nov–Dec, cool nights Jan-Mar, cool av. T Mar–Apr)	PC3 (warm captm/ captm-1)	PC4 (mixed)	PC5 (warm nights captm-1)
Haemaphysalis spp.	665.7	$E = -0.065$, $p = 0.019$	$E = 0.090$, $p = 0.018$	$E = 0.314$, $p = 0.007$	n.s.	n.s.
Schoutedenichia microcebi	445.3	n.s.	n.s.	n.s.	$E = -0.390$, $p = 2e\text{-}5$	$E = -1.729$, $p = 0.001$
Lemurpediculus spp.	615.2	$E = 0.064$, $p = 0.022$	$E = -0.198$, p = 3.74e-9	n.s.	$E = -0.200$, $p = 0.001$	$E = -0.744$, p = 6.46e–16
EPSR	1289.0	$E = -0.026$, $p = 0.041$	n.s.	$E = -0.047$, $p = 0.027$	$E = -0.091$, $p = 0.0006$	$E = -0.184$, p = 9.29e–7

Note: Table also includes an interpretation for each of the five principal components (in brackets), as derived from the climatic factors with high factor loadings (>0.7 or <−0.7, for details, see Table 5).
Abbreviations: AICc, corrected Akaike Information Criterion; av. T, average monthly temperature; captm, capture month; captm-1, month before capture, E, estimate; EPSR, Ectoparasite Species Richness; GLMM, generalized linear mixed model; n.s., not significant.

microcebi did not differ between sexes (Supporting Information: Table S6: both global models, p = n.s.). Significant effects of host age were neither found for the modeled ectoparasite taxa nor for EPSR (Table 4).

Body mass had a significant impact on all modeled ectoparasite taxa, but not on EPSR (Table 4). Host body mass was positively associated with *Haemaphysalis* spp. infestations (Supporting Information: Table S5: global model A; $p < 0.0005$) and *S. microcebi* infestations (Supporting Information: Table S6: global model A: $p < 0.0005$). In contrast, host body mass was negatively associated with *Lemurpediculus* spp. infestations (Supporting Information: Table S7: global model A, $p < 0.0005$).

3.3 | Monthly and yearly dynamics in infestation risk

Significant effects of the variable month were detected in all best models and for all parasite taxa, but the effects differed between them (Table 4). *Haemaphysalis* spp. were frequently found from April to November, showing an infestation peak in the middle of the dry season, in August (Figure 2a). Infestation rates were significantly higher in July, August, and September compared to the other sampled months. March, April, and May were the months with the lowest infestation rates (Supporting Information: Table S5: global model A.2). *S. microcebi* was recorded from April to October with an infestation peak in June (Figure 2b). Infestation rates were significantly higher in May, June, July, and August than in other months (Supporting Information: Table S6: global model A). *Lemurpediculus* spp. were recorded during the entire study period but with varying frequencies between months (Figure 2c). GLMMs confirmed that infestation rates were significantly higher in October than in the other months except for March and November. Infestation rates in March, April, September, and November were also significantly higher than in May, June, July, and August (Supporting Information: Table S7: global model A). The modeling of the EPSR revealed significantly higher values from August to October in comparison to April, May, and June, but not compared to July and November (Supporting Information: Table S8: global model A; Figure 2d). Animals also showed significantly higher EPSR in July than in May.

Sampling year impacted the infestation rates of all three modeled parasite taxa and the EPSR significantly but in different ways (Table 4). Infestation rates for *Haemaphysalis* spp. were significantly higher in 2010 and 2011 than in 2015 and 2016 (Supporting Information: Table S5: global model B; Figure 3a). *S. microcebi* were found with the significantly highest infestation rates in 2011, followed by 2016 and then by 2010 and 2015, which did not differ from each other (Supporting Information: Table S6: global model B; Figure 3b). *Lemurpediculus* spp. showed the highest infestation rates in 2016, the lowest rates in 2011, and intermediate rates in 2010 and 2015 (Supporting Information: Table S7: global model B; Figure 3c). Highest EPSR was found in 2011 and 2016, and it was lowest in 2010

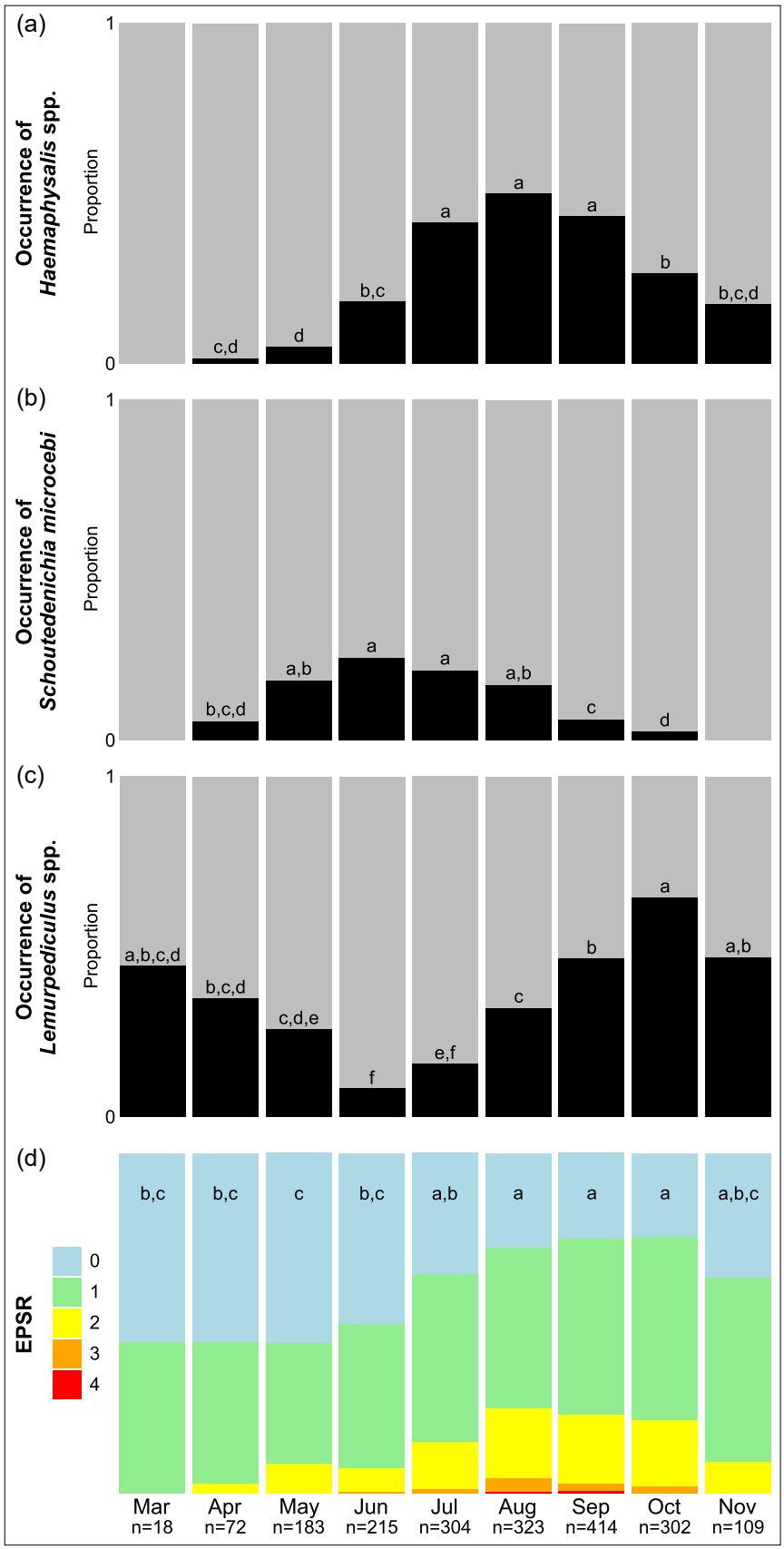

FIGURE 2 Proportion of mouse lemur ectoparasite inspections (total = 1940) showing infestation (occurrence: yes—in black, no—in gray) with modeled ectoparasite taxa, and distribution of ectoparasite species richness (ranging from 0 to 4 ectoparasite species detected on a host with color code) across all sampling months in Ampijoroa, Ankarafantsika National Park. (a) *Haemaphysalis* spp., (b) *Schoutedenichia microcebi*, (c) *Lemurpediculus* spp., (d) Ectoparasite species richness. *n*, number of ectoparasite inspections per month. Letter coding (a–d) indicates significant differences ($p < 0.05$) between months in the best model (see Table 4 and Supporting Information: Tables S5–S8 for details). For example, months marked with letter "a" are significantly different from months carrying other letters.

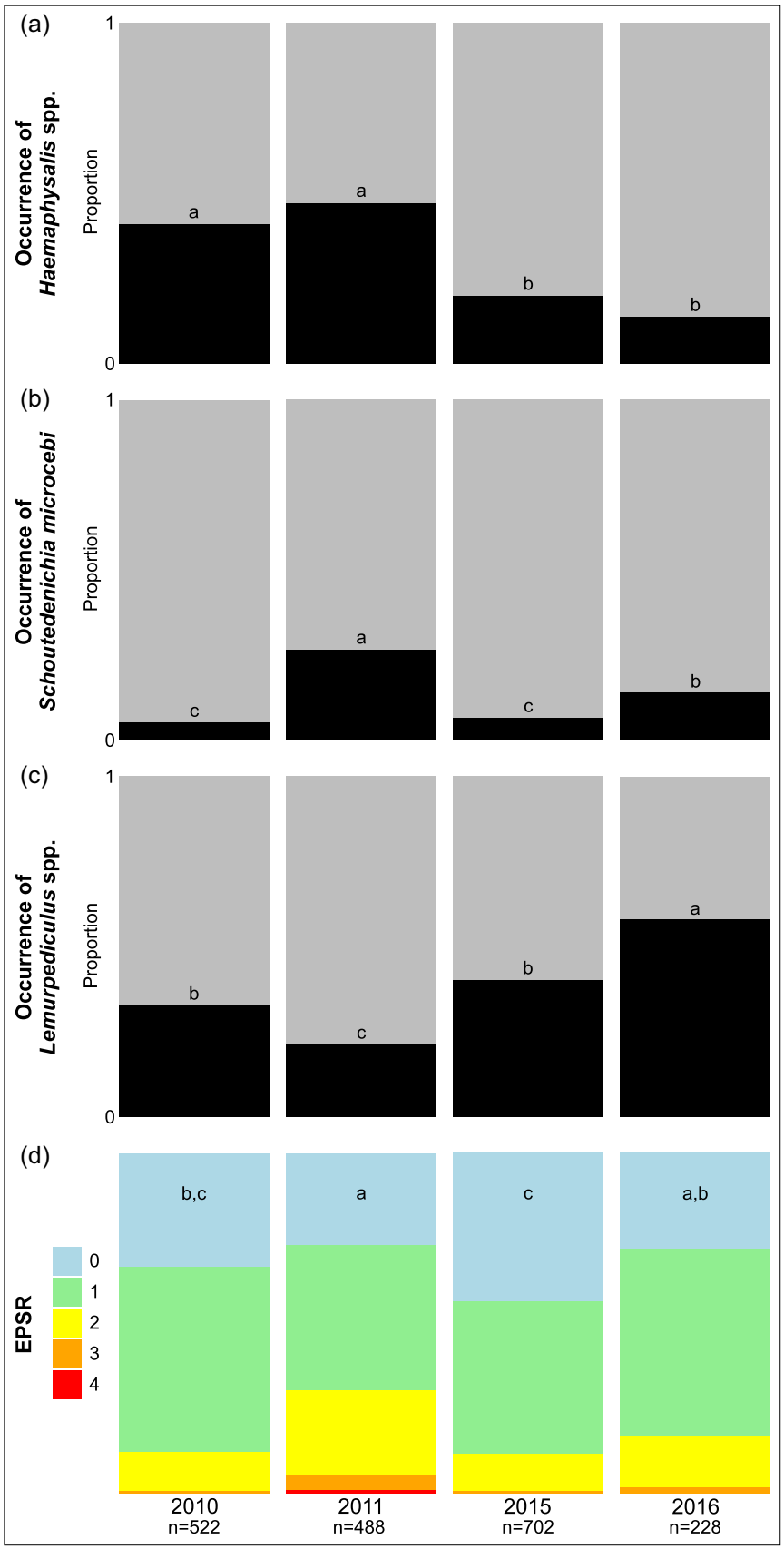

FIGURE 3 Proportion of mouse lemur ectoparasite inspections (total = 1940) showing infestation (occurrence: yes—in black, no—in gray) with modeled ectoparasite taxa, and distribution of ectoparasite species richness (ranging from 0 to 4 ectoparasite species detected on a host with color code) in the four sampling years in Ampijoroa, Ankarafantsika National Park. (a) *Haemaphysalis* spp., (b) *Schoutedenichia microcebi*, (c) *Lemurpediculus* spp., (d) Ectoparasite species richness. *n*, number of ectoparasite inspections. Letter coding (a–d) indicates significant differences ($p < 0.05$) between months in the best model (see Table 4 and Supporting Information: Tables S5–S8 for details). For example, months marked with letter "a" are significantly different from months carrying other letters.

and 2015, but without significant differences between 2016 and 2010 (Supporting Information: Table S8: global model B; Figure 3d).

3.4 | Effects of climatic variations on ectoparasite infestation risk

The first five PCs explained 96.61% of the total variance in the climate data set (Supporting Information: Table S3). PC1 and PC2 were best characterized by rainfall and temperature variations during the rainy season, while PC3 and PC5 showed the highest factor loadings for temperatures during the capture month and the month before capture, and PC4 represented a heterogeneous mix of all climatic factors (Supporting Information: Table S4). The PCA revealed strong climatic variations between the study years that were associated to rainfall and temperature variations during the previous rainy season (Supporting Information: Figure S2).

GLMMs revealed significant effects of PCs for all ectoparasite taxa and for EPSR, but the effects differed between them (Table 5, further details in Supporting Information: Tables S9–S12). *Haemaphysalis* spp. infestation rates were negatively associated with PC1 and positively with PC2 and PC3. Among these, PC3 (=warm temperatures during capture month and the month before capture) had the highest estimate and, therefore, the highest impact on the infestation risk with ticks (Supporting Information: Table S9). PC4 (=overall component) and PC5 (=warm nights during month before capture) were negatively related with *S. microcebi* infestations, among which warm night temperatures during the month before capture had the strongest negative effect (Supporting Information: Table S10). For *Lemurpediculus* spp., infestation rates were positively associated with PC1, but negatively associated with PC2, PC4, and PC5. Among these, the negative effect of PC5 (=warm night temperatures during the month before capture) showed the strongest impact (Supporting Information: Table S11). Finally, EPSR was significantly and negatively associated with PC1, PC3, PC4, and PC5, of which again PC5 had the strongest impact (Supporting Information: Table S12). Taken together, it appears that the temperatures during the capture month and the month before capture (PC3/PC5) consistently explain variations in infestation rates in all three ectoparasite taxa, although the relationship was positive in the case of *Haemaphysalis* spp., and negative for *S. microcebi* and *Lemurpediculus* spp.

4 | DISCUSSION

Although five ectoparasite taxa were identified on mouse lemurs in this study, only three of them (*Haemaphysalis* spp., *S. microcebi*, *Lemurpediculus* spp.) had sufficiently high occurrences to be used for the subsequent modeling approaches. While temporal, that is, monthly and yearly, variations of ectoparasite infestations were found in this study and will be discussed with the results on the impact of the climatic variables below, this study also revealed an impact of habitat type (=sampling site), and several host-related factors (species, sex, body mass) on the three most abundant ectoparasite taxa and on EPSR.

4.1 | Impact of study site and host-related factors (species, sex, age, and body mass)

Previous studies have shown that habitat quality, host species, sex, and body mass impact ectoparasite infestations in the two studied mouse lemur species (Kiene et al., 2020; Klein et al., 2018). However, the comparison of ectoparasite infestations in two study sites with largely different ecology but under the same climatic dynamics (Chanu et al., 2012; Sehen et al., 2010) allowed us to test the differential effect of species and habitat across multiple years, while controlling for sex, age, and body mass.

Our results showed that study site and host species affected the three parasite taxa differently. While *Haemaphysalis* (tick) infestation rates were neither affected by species nor study site, study site did affect *S. microcebi* (chigger), and both species and study site affected *Lemurpediculus* spp. (sucking lice) infestation rates. In principle, study site effects may be caused by ecological differences in the respective microhabitats and/or in the population density of the host in each study site. However, host species effects may be caused either by differences in host biology or by ectoparasite host specificity.

Since Klein et al. (2018) detected a higher prevalence of ticks on *M. murinus* than on *M. ravelobensis* in JBA in 2015/2016, the lack of host species differences for *Haemaphysalis* spp. was unexpected. However, many tick species are not very host specific (Klompen et al., 1996), and Kiene et al. (2020) did not find differences in tick prevalences between the two mouse lemur hosts in a larger network of study sites in the same region. Likewise, the lack of study site differences for ticks is unexpected, since JBB is more humid than JBA and should, therefore, provide a more favorable environment for off-host tick survival than the drier JBA. Further studies on the microhabitat requirements of the environmental stages of this parasite, that is, by sampling tick stages directly in the forest environment, and more detailed characterization of the specific environmental conditions in each study site will be needed to better understand its biology.

S. microcebi infestation rates were higher in *M. ravelobensis* inhabiting JBB than those from JBA, and higher than in *M. murinus* from JBA. Neither in JBA, nor in JBB, were differences between host species found. These results support an effect of study site but not of host species for this ectoparasite taxon. Since trombiculid mites are temporary parasites that spend most of their life cycle off the host and in leaf litter or soil (Sasa, 1961; Shatrov & Kudryashova, 2006), it is not surprising that study site, that is, the different habitat conditions in JBA and JBB, significantly affected its occurrence. In tropical regions, it has been shown that trombiculid mites are limited by precipitation and humidity (Sasa, 1961). Although precipitation does not differ between JBA and JBB as they are only 3 km apart, the forest in JBB is generally more humid than JBA due to its proximity to Lake Ravelobe (Sehen et al., 2010). This aspect could make JBB a

more suitable habitat for *S. microcebi* than JBA. Future comparative studies on the microclimate in each study site and the microhabitat requirements of the environmental stages of this chigger will be needed to fully understand the causal abiotic and biotic factors that drive spatial variations in mouse lemur infestations with trombiculid mites.

Concordant with previous findings for JBA during the 2015/2016 field season, *Lemurpediculus* spp. infestation rate was higher in *M. ravelobensis* than in *M. murinus*, which was previously explained with a higher degree of group sleeping and different composition of sleeping groups of *M. ravelobensis* compared to *M. murinus*, at least during those study years (Klein et al., 2018). In contrast to *S. microcebi*, infestation with *Lemurpediculus* lice was higher in JBA than in JBB, which may have resulted from differences in host population density between JBA and JBB. Many studies relate high host population densities to higher transmission rates, higher parasite prevalence, and higher parasite species richness (Arneberg, 2002; Krawczyk et al., 2020; Stringer & Linklater, 2015). A recent study from JBB suggested a substantial population decline for *M. ravelobensis* in JBB between 2010 and 2016 based long-term trapping data (Henkel et al., 2019/2020), which may have led to low louse transmission rates, and as a consequence, to low infestation rates in JBB.

Host sex has been shown to influence ectoparasite infestation susceptibility in many taxa (Fagir et al., 2015; de Mendonça et al., 2020; Zohdy et al., 2017) including *Lemurpediculus madagascariensis* infestation of *M. murinus* in JBA in 2010/2011 (Durden et al., 2021). Conversely, the study of Klein et al. (2018) on both mouse lemur species in JBA found no difference in infestation rates of male and female hosts for any of the studied ectoparasite taxa in the years 2015/2016, although males with large testes had a higher likelihood of a sucking lice infestation than males with small testes. Similarly, Kiene et al. (2020) found no effect of host sex on tick and mite infestations, but confirmed such an effect for sucking lice infestation, being higher in males than in females. Our study, which integrates and expands the datasets of both Durden et al. (2021) and Klein et al. (2018), did indeed detect higher infestation rates in male than in female mouse lemurs for *Haemaphysalis* spp., *Lemurpediculus* spp. and for EPSR. Whether these differences are due to testosterone-mediated differences in immunity or to sex-specific patterns of behavior, seasonal ranging and, therefore, exposure to these parasites (Klein, 2004; Muehlenbein & Watts, 2010; Waterman et al., 2014; Zohdy et al., 2012) cannot be clarified without further detailed integrative studies.

In our study, body mass was negatively associated with *Lemurpediculus* spp. infestation, but positively associated with *Haemaphysalis* spp. and *S. microcebi* prevalences. Given that the body mass of mouse lemurs was previously shown to decrease significantly over the course of the dry season (Klein et al., 2018), when food availability is low and reproductive activities start (Radespiel et al., 2021), it is not possible to disentangle the drivers of the negative relationship between body mass and sucking lice infestation, in particular, since they are nonexclusive.

The positive relationship between body mass and *Haemaphysalis* spp. and *S. microcebi* infestation shown in this study were not reported in the previous studies by Klein et al. (2018) and Kiene et al. (2020). Given that host body mass significantly impacted infestation rates for ticks and mites only when the study year was not part of the model, the influence of body mass may indirectly reflect year-to-year variations in body condition than, for example, choosiness of temporary parasites for a well-fed host (Christe et al., 2003).

4.2 | Temporal dynamics in parasite infestation rates

4.2.1 | Monthly dynamics

All three analyzed parasite taxa in this study showed persistent monthly variations in infestation patterns. *Haemaphysalis* ticks were found most frequently from April to November and had an infestation peak in August. The great majority of the collected specimen were larvae or nymphs, with only 15 adult *Haemaphysalis* spp. (of a total of more than 700 ticks) being found on *Microcebus* (Klein et al., 2018; personal observation). These results are congruent with previous findings by Klein et al. (2018) showing that tick infestation prevalences on mouse lemurs increased over the dry season, when food resources are less abundant (Thorén et al., 2011), and lemurs may need to descend more often to the floor while foraging. This might increase exposure to these parasites, which are usually in the lower vegetation questing for hosts (Walker et al., 2003). Low infestation intensities during the months March, April, and May might be related to the univoltine life cycle of *Haemaphysalis* spp. and its highly seasonal development, as described by Rodriguez et al. (2015). Klein et al. (2018) also suggested that adult ticks may mostly occur during the rainy season, when high humidity provides a favorable environment for egg development and hatching success (Randolph, 2004). Further, infestation rates were (at least partly) associated with warmer temperatures during the capture month and the month before capture, which might reflect that ticks need to find a host to avoid desiccation (Benoit & Denlinger, 2010; Randolph, 2004; Walker et al., 2003).

Since the only parasitic stage in chigger mites is the larva, these mites spend most of their life cycle in the environment (Mullen & O'Connor, 2019; Sasa, 1961; Shatrov & Kudryashova, 2006; Wall & Shearer, 2001a). In our study, *S. microcebi* chiggers were found on mouse lemurs mainly from April to October, with an infestation peak in June. Since egg development is likely the most susceptible stage to desiccation, eggs are probably deposited during the rainy season, and hence larvae should increasingly search for hosts over the first months of the dry season (Sasa, 1961).

Because sucking lice are permanent parasites and spend their entire life cycle on the host, it is not surprising that *Lemurpediculus* spp. were present during all months of the study period. However, louse infestation rates significantly increased from June to October. Similar seasonal trends have been reported previously for

Lemurpediculus spp. parasitizing *M. murinus* and *M. ravelobensis* by Klein et al. (2018), brown mouse lemurs (*M. rufus*) by Zohdy et al. (2012), and gray mouse lemurs (*M. murinus*) by Durden et al. (2021). The increase in *Lemurpediculus* spp. infestation rates coincides with the prebreeding and mating season of both mouse lemur species (Rina Evasoa et al., 2018). As discussed before, increased encounters between individuals and hormonal changes during this time of the year may have an important impact on sucking louse transmission and infestation susceptibility.

4.2.2 | Yearly dynamics and impact of climatic variations on ectoparasite infestation risk

Our data showed significant long-term variations in *Haemaphysalis* spp., *S. microcebi*, and *Lemurpediculus* spp. infestation rates, but each of them peaked in different years and were impacted by climatic variables in different ways.

Infestation rates for *Haemaphysalis* spp. were higher in 2010 and 2011 than in 2015 and 2016, which seemed to be related to several climate variables of both rainfall and temperature during the rainy season (PC1, PC2) but mostly to temperatures during the capture month and the month before capture (PC3). Cumming (2002) studied the effect of environmental variables on tick distributions in Africa and noted that tick survival and reproduction were not dependent on only one climatic variable, but that several variables together (such as monthly temperatures and rainfall) were better predictors. Other studies have also related tick development and survival to weather conditions and emphasized the high susceptibility of ticks to desiccation (Berger et al., 2014; Randolph & Storey, 1999; Walker et al., 2003). Since *Haemaphysalis* ticks are temporary parasites and spend most of the rainy season in the environment (Klein et al., 2018; Rodriguez et al., 2015), it was expected that low temperatures and high rainfall during the previous rainy season would have positively impacted the infestation risk. However, in contrast to these predictions, day temperatures during the month of capture and the month before capture had the strongest effect on the infestation risk with *Haemaphysalis* ticks which was higher when day temperatures were higher. Whether higher environmental temperatures may have accelerated tick development that may in turn have led to reduced intervals between parasitic periods or have increased the need of ticks to find a host to avoid desiccation cannot be clarified here. Lack of knowledge of exact egg-laying and hatching periods and environmental requirements of the different stages of *Haemaphysalis* spp. in the dry deciduous forests of northwestern Madagascar preclude a full understanding of their life cycle and the abiotic factors driving their host infestation patterns.

It has been stated that the development and survival of chiggers in tropical environments depends mostly on humidity and rainfall (Sasa, 1961; Wall & Shearer, 2001a). These mites spend most of their life cycle in the leaf litter or soil, and their successful reproduction, parts of their development and survival depend on specific environmental conditions in that particular forest stratum (Schöler, 2003). In our study, *S. microcebi* infestation rates were highest in 2011 and lowest in 2010 and 2015. Our expectation of higher infestations under lower temperatures and in years of more rainfall was only partially supported. Only one climatic variable was clearly identified impacting chigger infestation risk significantly: infestation risk increased with lower overnight temperatures during the month before capture (=PC5). Because corresponding data on humidity, soil temperatures, and moisture in the study sites are not currently available, and we lack knowledge of the environmental requirements of the different stages of *S. microcebi*, causal explanations for abiotic effects on *S. microcebi* survival, reproduction, and resulting infestation risks for hosts cannot be currently identified. Moreover, complex indirect effects, such as impacts of climatic variations on plant phenology and leaf litter, may also shape conditions in the microhabitats of these parasites (Anu et al., 2009) and require further investigation.

We expected the directly transmitted (host to host) sucking lice to be least impacted by year-to-year environmental changes, although it has previously been shown that UV radiation and aridity might have negative consequences for sucking lice development and survival (Durden & Musser, 1994; Kiene et al., 2020; Moyer et al., 2002; Wall & Shearer, 2001a). Our modeling results revealed that *Lemurpediculus* spp. showed distinct yearly variations, with highest infestation rates in 2016, followed by 2010/2015, and then 2011. Therefore, and in contrast to our expectations, sucking louse infestation risk was highly impacted by climatic variations, both by variations in rainfall and temperature during the rainy season (PC1, PC2), and by temperatures during the months during and before host capture (PC5). Whether sucking lice responded to these environmental changes directly or indirectly, that is, if the environmental changes impacted the lice directly by modifying their microenvironment in the fur of the hosts or by impacting the ecology (e.g., feeding strategies, shelter use) and behavior of the host species and in consequence modulated social encounter, parasite removal or transmission opportunities for sucking lice, needs to be investigated in future studies.

Taken together, this study shows that several host-related (species, sex, body mass), environmental and temporal factors (study site, month, year, climate conditions) influence the infestation dynamics of three native Malagasy ectoparasite taxa (*Haemaphysalis* spp., *S. microcebi*, and *Lemurpediculus* spp.) on two mouse lemur host species (*M. murinus*, *M. ravelobensis*) in different and complex ways. Differences in host-parasite relationships can be best explained by differences between parasite life cycles and associated infection and infestation pathways. Most importantly, this study provided evidence for strong year-to-year fluctuations in ectoparasite infestation rates, with the direction of change varying substantially between parasite taxa. Such fluctuations can be easily overlooked with short-term research projects. Due to multivariate and complex climatic and biotic interactions in seasonal ecosystems like the western dry deciduous forests of Madagascar, comprehensive long-term studies across a series of years including both host-related and environmental factors, as well as additional data such as abiotic

factors in leaf litter and soil, and biotic factors regarding the vegetation, phenology, sleeping sites, or population density, are needed to disentangle causes and consequences of yearly fluctuations within these biological networks of hosts and parasites within their seasonal ecosystems. This is more relevant than ever in times of ongoing and strong anthropogenic pressures and alarming climate change scenarios that are already affecting Madagascar with its highly fragmented and vulnerable forest remnants (Ingram & Dawson, 2005; Vieilledent et al., 2018).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Specimens are stored in the collection of the Institute of Zoology, University of Veterinary Medicine Hannover, Germany, and can be accessed upon reasonable request. Data generated in the course of this study are openly available in Zenodo under doi.10.5281/zenodo.7766549. All results of the statistical analyses are deposited as Supporting Information.

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REFERENCES

Akinyi, M. Y., Tung, J., Jeneby, M., Patel, N. B., Altmann, J., & Alberts, S. C. (2013). Role of grooming in reducing tick load in wild baboons (*Papio cynocephalus*). *Animal Behaviour*, *85*(3), 559–568. https://doi.org/10.1016/j.anbehav.2012.12.012

Altizer, S., Nunn, C. L., & Lindenfors, P. (2007). Do threatened hosts have fewer parasites? A comparative study in primates. *Journal of Animal Ecology*, *76*(2), 304–314. https://doi.org/10.1111/j.1365-2656.2007.01214.x

Anu, A., Sabu, T. K., & Vineesh, P. (2009). Seasonality of litter insects and relationship with rainfall in a wet evergreen forest in south western Ghats. *Journal of Insect Science*, *9*(46), 1–10. https://doi.org/10.1673/031.009.4601

Arneberg, P. (2002). Host population density and body mass as determinants of species richness in parasite communities: Comparative analyses of directly transmitted nematodes of mammals. *Ecography*, *25*(1), 88–94. https://doi.org/10.1034/j.1600-0587.2002.250110.x

Attanasio, R., Brasky, K. M., Robbins, S. H., Jayashankar, L., Nash, R. J., & Butler, T. M. (2001). Age-related autoantibody production in a nonhuman primate model. *Clinical and Experimental Immunology*, *123*(3), 361–365. https://doi.org/10.1046/j.1365-2249.2001.01454.x

Barrett, M. A., Brown, J. L., Junge, R. E., & Yoder, A. D. (2013). Climate change, predictive modeling and lemur health: Assessing impacts of changing climate on health and conservation in Madagascar. *Biological Conservation*, *157*, 409–422. https://doi.org/10.1016/j.biocon.2012.09.003

Barton, K. (2020). MuMIn: Multi-model inference. R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Beldomenico, P. M., & Begon, M. (2010). Disease spread, susceptibility and infection intensity: Vicious circles? *Trends in Ecology & Evolution*, *25*(1), 21–27. https://doi.org/10.1016/j.tree.2009.06.015

Benoit, J. B., & Denlinger, D. L. (2010). Meeting the challenges of on-host and off-host water balance in blood-feeding arthropods. *Journal of Insect Physiology*, *56*(10), 1366–1376. https://doi.org/10.1016/j.jinsphys.2010.02.014

Berger, K. A., Ginsberg, H. S., Gonzalez, L., & Mather, T. N. (2014). Relative humidity and activity patterns of *Ixodes scapularis* (Acari: Ixodidae). *Journal of Medical Entomology*, *51*(4), 769–776. https://doi.org/10.1603/ME13186

Blersch, R., Bonnell, T. R., Barrett, L., & Henzi, S. P. (2021). Seasonal effects in gastrointestinal parasite prevalence, richness and intensity in vervet monkeys living in a semi-arid environment. *Journal of Zoology*, *314*(3), 163–173. https://doi.org/10.1111/jzo.12877

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. Springer. https://doi.org/10.1007/b97636

Chanu, L., Goetze, D., Rajeriarison, C., Roger, E., Thorén, S., Porembski, S., & Radespiel, U. (2012). Can differences in floristic composition explain variation in the abundance of two sympatric mouse lemur species (*Microcebus*) in the Ankarafantsika National Park, northwestern Madagascar? *Malagasy Nature*, *6*, 83–102.

Chapman, C. A., Gillespie, T. R., & Goldberg, T. L. (2005). Primates and the ecology of their infectious diseases: How will anthropogenic change affect host-parasite interactions? *Evolutionary Anthropology: Issues, News, and Reviews*, *14*(4), 134–144. https://doi.org/10.1002/evan.20068

Chapman, C. A., Speirs, M. L., Gillespie, T. R., Holland, T., & Austad, K. M. (2006). Life on the edge: Gastrointestinal parasites from the forest edge and interior primate groups. *American Journal of Primatology*, *68*(4), 397–409. https://doi.org/10.1002/ajp

Christe, P., Giorgi, M. S., Vogel, P., & Arlettaz, R. (2003). Differential species-specific ectoparasitic mite intensities in two intimately coexisting sibling bat species: Resource-mediated host attractiveness or parasite specialization? *Journal of Animal Ecology*, *72*(5), 866–872. https://doi.org/10.1046/j.1365-2656.2003.00759.x

Clough, D., Heistermann, M., & Kappeler, P. M. (2010). Host intrinsic determinants and potential consequences of parasite infection in free-ranging red-fronted lemurs (*Eulemur fulvus rufus*). *American Journal of Physical Anthropology*, *142*(3), 441–452. https://doi.org/10.1002/ajpa.21243

Cumming, G. S. (2002). Comparing climate and vegetation as limiting factors for species ranges of African ticks. *Ecology*, *83*(1), 255–268. https://doi.org/10.1890/0012-9658(2002)083[0255:CCAVAL]2.0.CO;2

Durden, L. A., Kessler, S. E., Radespiel, U., Hasiniaina, A. F., Stekolnikov, A. A., Chalkowski, K., & Zohdy, S. (2021). Host associations of ectoparasites of the gray mouse lemur, *Microcebus murinus*, in Northwestern Madagascar. *The Journal of Parasitology*, *107*(1), 108–114. https://doi.org/10.1645/20-145

Durden, L. A., Kessler, S. E., Radespiel, U., Zimmermann, E., Hasiniaina, A. F., & Zohdy, S. (2018). A new species of sucking louse (Phthiraptera: Anoplura: Polyplacidae) from the gray mouse lemur, *Microcebus murinus* (Primates: Cheirogaleidae), in Madagascar. *Journal of Medical Entomology*, *55*(4), 910–914. https://doi.org/10.1093/jme/tjy046

Durden, L. A., & Musser, G. G. (1994). The sucking lice (Insecta, Anoplura) of the world—A taxonomic checklist with records of mammalian hosts and geographical distributions. *Bulletin of the American Museum of Natural History*, *218*, 1–90.

Ehlers, J., Poppert, S., Ratovonamana, R. Y., Ganzhorn, J. U., Tappe, D., & Krüger, A. (2019). Ectoparasites of endemic and domestic animals in southwest Madagascar. *Acta Tropica*, *196*, 83–92. https://doi.org/10.1016/j.actatropica.2019.05.008

Fagir, D. M., Horak, I. G., Ueckermann, E. A., Bennett, N. C., & Lutermann, H. (2015). Ectoparasite diversity in the Eastern Rock Sengis (*Elephantulus myurus*): The effect of seasonality and host sex. *African Zoology*, *50*(2), 109–117. https://doi.org/10.1080/15627020.2015.1021173

Foerster, M., Delgado, I., Abraham, K., Gerstmayr, S., & Neubert, R. (1997). Comparative study on age-dependent development of surface receptors on peripheral blood lymphocytes in children and young nonhuman primates. *Life Sciences*, *60*(10), 773–785. https://doi.org/10.1016/S0024-3205(97)00005-2

Gillespie, T. R., & Chapman, C. A. (2008). Forest fragmentation, the decline of an endangered primate, and changes in host-parasite interactions relative to an unfragmented forest. *American Journal of Primatology*, *70*(3), 222–230. https://doi.org/10.1002/ajp.20475

Haberthur, K., Engelman, F., Barron, A., & Messaoudi, I. (2010). Immune senescence in aged nonhuman primates. *Experimental Gerontology*, *45*(9), 655–661. https://doi.org/10.1016/j.exger.2010.06.001

Henkel, H., Zimmermann, E., Klein, A., Randrianambinina, B., Rasoloharijaona, S., Rakotondravony, R., Mester, S., & Radespiel, U. (2019/2020). Indications of a potential alarming population decline in the golden-brown mouse lemur (*Microcebus ravelobensis*) in a long-term study site in the Ankarafantsika National Park. *Lemur News*, *22*, 51–53.

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, *50*(3), 346–363. https://doi.org/10.1002/bimj.200810425

Ingram, J. C., & Dawson, T. P. (2005). Climate change impacts and vegetation response on the island of Madagascar. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, *363*(1826), 55–59. https://doi.org/10.1098/rsta.2004.1476

Irwin, M. T., & Raharison, J. L. (2009). A review of the endoparasites of the lemurs of Madagascar. *Malagasy Nature*, *2*, 66–93.

Ishii, N., Kato, T., Uno, T., Tanaka, I., Kajigaya, H., & Hayama, S. (2017). The number of louse eggs on wild Japanese macaques (*Macaca fuscata*) varies with age, but not with sex or season. *International Journal of Primatology*, *38*(6), 1090–1101. https://doi.org/10.1007/s10764-017-9998-1

Kiene, F., Andriatsitohaina, B., Ramsay, M. S., Rakotondramanana, H., Rakotondravony, R., Radespiel, U., & Strube, C. (2020). Forest edges affect ectoparasite infestation patterns of small mammalian hosts in fragmented forests in Madagascar. *International Journal for Parasitology*, *50*(4), 299–313. https://doi.org/10.1016/j.ijpara.2020.01.008

Kiene, F., Andriatsitohaina, B., Ramsay, M. S., Rakotondravony, R., Strube, C., & Radespiel, U. (2021). Habitat fragmentation and vegetation structure impact gastrointestinal parasites of small mammalian hosts in Madagascar. *Ecology and Evolution*, *11*(11), 6766–6788. https://doi.org/10.1002/ece3.7526

Klein, A., Zimmermann, E., Radespiel, U., Schaarschmidt, F., Springer, A., & Strube, C. (2018). Ectoparasite communities of small-bodied Malagasy primates: Seasonal and socioecological influences on tick, mite and lice infestation of *Microcebus murinus* and *M. ravelobensis* in northwestern Madagascar. *Parasites & Vectors*, *11*(1), 459. https://doi.org/10.1186/s13071-018-3034-y

Klein, S. L. (2004). Hormonal and immunological mechanisms mediating sex differences in parasite infection. *Parasite Immunology*, *26*(6–7), 247–264. https://doi.org/10.1111/j.0141-9838.2004.00710.x

Klompen, J. S. H., Black, IV, W. C., Keirans, J. E., & Oliver, J. H. (1996). Evolution of ticks. *Annual Review of Entomology*, *41*(1), 141–161. https://doi.org/10.1146/annurev.en.41.010196.001041

Krawczyk, A. I., Van Duijvendijk, G. L. A., Swart, A., Heylen, D., Jaarsma, R. I., Jacobs, F. H. H., Fonville, M., Sprong, H., & Takken, W. (2020). Effect of rodent density on tick and tick-borne pathogen populations: Consequences for infectious disease risk. *Parasites & Vectors*, *13*(1), 34. https://doi.org/10.1186/s13071-020-3902-0

de Mendonça, R. F. B., Colle, A. C., Freitas, L. C., Martins, T. F., Horta, M. C., Oliveira, G. M. B., Pacheco, R. C., Mateus, L. A. F., & Rossi, R. V. (2020). Ectoparasites of small mammals in a fragmented area of the southern Amazonia: Interaction networks and correlations with seasonality and host sex. *Experimental and Applied Acarology*, *81*(1), 117–134. https://doi.org/10.1007/s10493-020-00491-5

Mittermeier, R. A., Louis, E. E., Jr., Richardson, M., Schwitzer, C., Langrand, O., Rylands, A., Hawkins, F., Rajaobelina, S., Ratsimbazafy, J., Rasoloarison, R., Roos, C., Kappeler, P. M., & Mackinnon, J. (2010). *Lemurs of Madagascar*. Conservation International.

Moyer, B. R., Drown, D. M., & Clayton, D. H. (2002). Low humidity reduces ectoparasite pressure: Implications for host life history evolution. *Oikos*, *97*(2), 223–228. https://doi.org/10.1034/j.1600-0706.2002.970208.x

Muehlenbein, M. P., & Watts, D. P. (2010). The costs of dominance: Testosterone, cortisol and intestinal parasites in wild male chimpanzees. *BioPsychoSocial Medicine*, *4*, 21. https://doi.org/10.1186/1751-0759-4-21

Mullen, G. R., & O'Connor, B. M. (2019). Mites (Acari). In G. R. Mullen & L. A. Durden (Eds.), *Medical and veterinary entomology* (pp. 533–602). Academic Press. https://doi.org/10.1016/B978-0-12-814043-7.00026-1

Palacios, M. G., Cunnick, J. E., Winkler, D. W., & Vleck, C. M. (2007). Immunosenescence in some but not all immune components in a free-living vertebrate, the tree swallow. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1612), 951–957. https://doi.org/10.1098/rspb.2006.0192

Patterson, J. E. H., & Ruckstuhl, K. E. (2013). Parasite infection and host group size: A meta-analytical review. *Parasitology*, *140*(7), 803–813. https://doi.org/10.1017/S0031182012002259

Pedersen, A. B., Altizer, S., Poss, M., Cunningham, A. A., & Nunn, C. L. (2005). Patterns of host specificity and transmission among parasites of wild primates. *International Journal for Parasitology*, *35*(6), 647–657. https://doi.org/10.1016/j.ijpara.2005.01.005

Petrzelková, K. J., Hasegawa, H., Appleton, C. C., Huffman, M. A., Archer, C. E., Moscovice, L. R., Mapua, M. I., Singh, J., & Kaur, T. (2010). Gastrointestinal parasites of the chimpanzee population introduced onto Rubondo Island National Park, Tanzania. *American Journal of Primatology*, *72*(4), 307–316. https://doi.org/10.1002/ajp.20783

Radespiel, U., Cepok, S., Zietemann, V., & Zimmermann, E. (1998). Sex-specific usage patterns of sleeping sites in grey mouse lemurs (*Microcebus murinus*) in northwestern Madagascar. *American Journal of Primatology*, *46*(1), 77–84. https://doi.org/10.1002/(SICI)1098-2345(1998)46:1<77::AID-AJP6>3.0.CO;2-S

Radespiel, U., Ehresmann, P., & Zimmermann, E. (2003). Species-specific usage of sleeping sites in two sympatric mouse lemur species (*Microcebus murinus* and *M. ravelobensis*) in northwestern Madagascar. *American Journal of Primatology*, *59*(4), 139–151. https://doi.org/10.1002/ajp.10071

Radespiel, U., Rakotondravony, R., Rasoloharijaona, S., & Randrianambinina, B. (2021). A 24-Year record of female reproductive dynamics in two sympatric mouse lemur species in northwestern Madagascar. *International Journal of Primatology*, *43*, 559–583. https://doi.org/10.1007/s10764-021-00261-z

Raharivololona, B., & Ganzhorn, J. (2009). Gastrointestinal parasite infection of the Gray mouse lemur (*Microcebus murinus*) in the littoral forest of Mandena, Madagascar: Effects of forest fragmentation and degradation. *Madagascar Conservation & Development*, *4*(2), 104–112. https://doi.org/10.4314/mcd.v4i2.48650

Rakotondravony, R., & Radespiel, U. (2009). Varying patterns of coexistence of two mouse lemur species (*Microcebus ravelobensis* and *M. murinus*) in a heterogeneous landscape. *American Journal of Primatology*, *71*(11), 928–938. https://doi.org/10.1002/ajp.20732

Randolph, S. E. (2004). Tick ecology: Processes and patterns behind the epidemiological risk posed by ixodid ticks as vectors. *Parasitology*, *129*(S1), S37–S65. https://doi.org/10.1017/S0031182004004925

Randolph, S. E., & Storey, K. (1999). Impact of microclimate on immature tick-rodent host interactions (Acari: Ixodidae): Implications for parasite transmission. *Journal of Medical Entomology*, *36*(6), 741–748. https://doi.org/10.1093/jmedent/36.6.741

Rendigs, A., Radespiel, U., Wrogemann, D., & Zimmermann, E. (2003). Relationship between microhabitat structure and distribution of mouse lemurs (*Microcebus spp.*) in northwestern Madagascar. *International Journal of Primatology*, *24*(1), 47–64. https://doi.org/10.1023/A:1021494428294

Renwick, A. R., & Lambin, X. (2013). Host-parasite interactions in a fragmented landscape. *International Journal for Parasitology*, *43*(1), 27–35. https://doi.org/10.1016/j.ijpara.2012.10.012

Rina Evasoa, M., Radespiel, U., Hasiniaina, A. F., Rasoloharijaona, S., Randrianambinina, B., Rakotondravony, R., & Zimmermann, E. (2018). Variation in reproduction of the smallest-bodied primate radiation, the mouse lemurs (*Microcebus spp.*): A synopsis. *American Journal of Primatology*, *80*(7), e22874. https://doi.org/10.1002/ajp.22874

Rodriguez, I. A., Rasoazanabary, E., & Godfrey, L. R. (2015). Seasonal variation in the abundance and distribution of ticks that parasitize *Microcebus griseorufus* at the Bezà Mahafaly Special Reserve, Madagascar. *International Journal for Parasitology: Parasites and Wildlife*, *4*, 408–413. https://doi.org/10.1016/j.ijppaw.2015.10.007

Rondón, S., Ortiz, M., León, C., Galvis, N., Link, A., & González, C. (2017). Seasonality, richness and prevalence of intestinal parasites of three neotropical primates (*Alouatta seniculus*, *Ateles hybridus* and *Cebus versicolor*) in a fragmented forest in Colombia. *International Journal for Parasitology: Parasites and Wildlife*, *6*(3), 202–208. https://doi.org/10.1016/j.ijppaw.2017.07.006

Sasa, M. (1961). Biology of chiggers. *Annual Review of Entomology*, *6*, 221–244. https://doi.org/10.1146/annurev.en.06.010161.001253

Schöler, A. (2003). *Untersuchungen zur Biologie und Ökologie der Herbstmilbe Neotrombicula autumnalis (Acari: Trombiculidae) im Hinblick auf Bekämpfungsmöglichkeiten sowie zu ihrer Bedeutung als Vektor der Borreliose* [Unpublished doctoral dissertation]. Rheinische Friedrich-Wilhelms-University Bonn.

Schwitzer, C., Mittermeier, R. A., Johnson, S. E., Donati, G., Irwin, M., Peacock, H., Ratsimbazafy, J., Razafindramanana, J., Louis, E. E., Chikhi, L., Colquhoun, I. C., Tinsman, J., Dolch, R., LaFleur, M., Nash, S., Patel, E., Randrianambinina, B., Rasolofoharivelo, T., & Wright, P. C. (2014). Averting Lemur extinctions amid Madagascar's political crisis. *Science*, *343*(6173), 842–843. https://doi.org/10.1126/science.1245783

Schwitzer, N., Clough, D., Zahner, H., Kaumanns, W., Kappeler, P., & Schwitzer, C. (2010). Parasite prevalence in blue-eyed black lemurs *Eulemur flavifrons* in differently degraded forest fragments. *Endangered Species Research*, *12*(3), 215–225. https://doi.org/10.3354/esr00304

Sehen, L., Goetze, D., Rajeriarison, C., Roger, E., Thorén, S., & Radespiel, U. (2010). Structural and floristic traits of habitats with differing relative abundance of the lemurs *Microcebus murinus* and *M. ravelobensis* in Northwestern Madagascar. *Ecotropica*, *16*(1), 15–30.

Shatrov, A. B., & Kudryashova, N. I. (2006). Taxonomy, life cycles and the origin of parasitism in trombiculid mites. In S. Morand, B. R. Krasnov, & R. Poulin (Eds.), *Micromammals and Macroparasites* (pp. 119–140). Springer. https://doi.org/10.1007/978-4-431-36025-4_8

Springer, A., Durden, L. A., Kiene, F., Klein, A., Rakotondravony, R., Ehlers, J., Greiman, S. E., Blanco, M. B., Zohdy, S., Kessler, S. E., Strube, C., & Radespiel, U. (2023). Molecular phylogenetics of the sucking louse genus *Lemurpediculus* (Insecta: Phthiraptera), ectoparasites of lemurs, with descriptions of three new species. *International Journal for Parasitology: Parasites and Wildlife*, *20*, 138–152. https://doi.org/10.1016/j.ijppaw.2023.02.002

Springer, A., & Kappeler, P. M. (2016). Intestinal parasite communities of six sympatric lemur species at Kirindy Forest, Madagascar. *Primate Biology*, *3*(2), 51–63. https://doi.org/10.5194/pb-3-51-2016

Stekolnikov, A. A. (2018). Taxonomy and distribution of African chiggers (Acariformes, Trombiculidae). *European Journal of Taxonomy*, *395*, 1–233. https://doi.org/10.5852/ejt.2018.395

Stekolnikov, A. A., Kessler, S. E., Matthee, S., Hasiniaina, A. F., Radespiel, U., Zimmermann, E., & Durden, L. A. (2019). A new species of *Schoutedenichia* Jadin & Vercammen-Grandjean, 1954 from Madagascar and a re-description of *S. dutoiti* (Radford, 1948) from South Africa (Acariformes: Trombiculidae). *Systematic Parasitology*, *96*(8), 703–713. https://doi.org/10.1007/s11230-019-09877-5

Stringer, A. P., & Linklater, W. L. (2015). Host density drives macroparasite abundance across populations of a critically endangered megaherbivore. *Oecologia*, *179*(1), 201–207. https://doi.org/10.1007/s00442-015-3319-1

Thorén, S., Quietzsch, F., Schwochow, D., Sehen, L., Meusel, C., Meares, K., & Radespiel, U. (2011). Seasonal changes in feeding ecology and activity patterns of two sympatric mouse lemur species, the gray mouse lemur (*Microcebus murinus*) and the golden-brown mouse lemur (*M. ravelobensis*), in northwestern Madagascar. *International Journal of Primatology*, *32*, 566–586. https://doi.org/10.1007/s10764-010-9488-1

Vieilledent, G., Grinand, C., Rakotomalala, F. A., Ranaivosoa, R., Rakotoarijaona, J. R., Allnutt, T. F., & Achard, F. (2018). Combining global tree cover loss data with historical national forest cover maps

to look at six decades of deforestation and forest fragmentation in Madagascar. *Biological Conservation*, *222*, 189–197. https://doi.org/10.1016/j.biocon.2018.04.008

Walker, A. R., Bouattour, A., Camicas, J., Estrada-Peña, A., Horak, I. G., Latif, A. A., Pegram, R., & Preston, P. M. (2003). *Ticks of domestic animals in Africa: A guide to identification of species*. Bioscience Reports.

Wall, R., & Shearer, D. (1997). Ticks (Acari), *Veterinary entomology: Arthropod ectoparasites of veterinary importance* (pp. 96–140). Chapman and Hall. https://doi.org/10.1007/978-94-011-5852-7_3

Wall, R., & Shearer, D. (2001a). Lice (Phthiraptera), *Veterinary ectoparasites: Biology, pathology and control* (pp. 162–178). Blackwell Science Ltd. https://doi.org/10.1002/9780470690505.ch7

Wall, R., & Shearer, D. (2001b). Mites (Acari), *Veterinary ectoparasites: Biology, pathology and control* (pp. 23–54). Blackwell Science Ltd. https://doi.org/10.1002/9780470690505.ch2

Waterman, J. M., Macklin, G. F., & Enright, C. (2014). Sex-biased parasitism in Richardson's ground squirrels (*Urocitellus richardsonii*) depends on the parasite examined. *Canadian Journal of Zoology*, *92*(1), 73–79. https://doi.org/10.1139/cjz-2013-0151

Whiteman, N. K., & Parker, P. G. (2005). Using parasites to infer host population history: A new rationale for parasite conservation. *Animal Conservation*, *8*(2), 175–181. https://doi.org/10.1017/S1367943005001915

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer.

Wikel, S. K. (1982). Immune responses to arthropods and their products. *Annual Review of Entomology*, *27*, 21–48. https://doi.org/10.1146/annurev.en.27.010182.000321

Zimmermann, E., Cepok, S., Rakotoarison, N., Zietemann, V., & Radespiel, U. (1998). Sympatric mouse lemurs in Nort-West Madagascar: A new rufous mouse lemur species (*Microcebus ravelobensis*). *Folia Primatologica*, *69*(2), 106–114. https://doi.org/10.1159/000021571

Zohdy, S. (2012). *Senescence ecology: Aging in a population of wild brown mouse lemurs (Microcebus rufus)* [Unpublished doctoral dissertation]. University of Helsinki.

Zohdy, S., Bisanzio, D., Tecot, S., Wright, P. C., & Jernvall, J. (2017). Aggression and hormones are associated with heterogeneity in parasitism and parasite dynamics in the brown mouse lemur. *Animal Behaviour*, *132*, 109–119. https://doi.org/10.1016/j.anbehav.2017.08.002

Zohdy, S., & Durden, L. A. (2016). A review of ectoparasites in the Cheirogaleidae. In S. M. Lehman, U. Radespiel, & E. Zimmermann (Eds.), *The Dwarf and Mouse Lemurs of Madagascar: Biology, Behavior and Conservation Biogeography of the Cheirogaleidae* (pp. 220–232). Cambridge University Press. https://doi.org/10.1017/CBO9781139871822.012

Zohdy, S., Kemp, A. D., Durden, L. A., Wright, P. C., & Jernvall, J. (2012). Mapping the social network: Tracking lice in a wild primate (*Microcebus rufus*) population to infer social contacts and vector potential. *BMC Ecology*, *12*, 4. https://doi.org/10.1186/1472-6785-12-4

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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