

## Ectoparasites of endemic and domestic animals in southwest Madagascar

Julian Ehlers<sup>a,b</sup>, Sven Poppert<sup>c,d</sup>, Rakotomalala Yedidya Ratovonamana<sup>a,e</sup>,  
Jörg Ulrich Ganzhorn<sup>a</sup>, Dennis Tappe<sup>b,\*</sup>, Andreas Krüger<sup>f,\*\*</sup>

<sup>a</sup> University of Hamburg, Department of Biology, Animal Ecology and Conservation, Hamburg, Germany

<sup>b</sup> Bernhard Nocht Institute for Tropical Medicine, Labgroup Zoonoses, Hamburg, Germany

<sup>c</sup> Swiss Tropical and Public Health Institute, Basel, Switzerland

<sup>d</sup> Faculty of Medicine, University Basel, Basel, Switzerland

<sup>e</sup> Department of Biology and Plant Ecology, Faculty of Science, University of Antananarivo, Antananarivo, Madagascar

<sup>f</sup> Bundeswehr Hospital Hamburg, Tropical Microbiology and Entomology Branch, Bernhard-Nocht-Strasse 74, 20359, Hamburg, Germany

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### ABSTRACT

Human encroachment of natural habitats bears the threat of disease transmission between native and introduced species that had not come into contact before, thus promoting the spread of new diseases in both directions. This is a matter of concern especially in areas where human-wildlife contact has not been intense in the recent past. In southwest Madagascar, we collected ectoparasites from various mammalian hosts and chicken, and examined their host preferences and their prevalence in relation to season and habitat degradation.

Field-work took place in the northern portion of Tsimanampetsotsa National Park and the adjacent coastal strip (littoral) in the dry and in the rainy season of 2016/2017. Endemic mammals were trapped with live traps placed in habitats of different degrees of degradation: 1) relatively pristine forest, 2) degraded forest, 3) cultivated and shrub land. Rats and mice were also trapped in 4) villages.

We identified 17 species of ectoparasites (296 individuals of ticks [5 species], 535 lice [7 spp.], 389 fleas [4 spp.] and 13 mites [1 sp.]) collected from 15 host species. There was no indication for seasonal or habitat effects on parasite infection. A large portion of the parasites was host-specific. Some ectoparasite species were shared either by several endemic or by several introduced species, but apart from the introduced flea species *Echidnophaga gallinacea* (collected from six different hosts including the endemic carnivore *Galidictis grandidieri*) no other ectoparasite species was shared between endemic and introduced host species.

### 1. Introduction

Driven by a rapidly growing human population (UNFPA, 2019), the destruction of forest habitats is a major concern in Madagascar (Miles et al., 2006; Harper et al., 2007; Ratovonamana et al., 2013; Brinkmann et al., 2014). The anthropogenic alteration of the environment and the increase in contact zones between anthropogenic and original habitats represents a potential threat for humans and wildlife alike, as new contacts are important drivers of the emergence of new diseases and their transmission between livestock, humans and wildlife (Daszak et al., 2000; Dobson and Foufopoulos, 2001; Köndgen et al., 2008; Gortazar et al., 2014; Plowright et al., 2015).

In Madagascar, studies on wildlife pathogens have focused on viral or bacterial disease transmission or intestinal endoparasites (Raharivololona et al., 2007; Irwin and Raharison, 2009; Wright et al.,

2009; Schwitzer et al., 2010; Bublitz et al., 2015; Radespiel et al., 2015; Zohdy et al., 2015; Rakotoniaina et al., 2016). Studies on ectoparasites are scant (reviewed by Klompen, 2003; O'Connor et al., 2003), and studies on lemur parasites (Junge and Louis, 2007; Dutton et al., 2008; Junge et al., 2008; Durden et al., 2010; Rodriguez et al., 2012; Klein et al., 2018) outnumber those of ectoparasites from non-lemur taxa, such as tenrecs (Apanaskevich et al., 2013) and rats (Brook et al., 2017) in recent years.

Interspecific interactions between parasites and hosts and the underlying dynamics remain unclear.

Ectoparasites can have a direct impact on the health of the infested animal by causing blood loss or skin lesions and inducing inflammatory responses (Brain and Bohrmann, 1992). Some tick species secrete toxins while feeding that may cause tick paralysis in the host, which is likely the severest of these direct reactions to ectoparasitic infestation, often

\* Corresponding author at: Bernhard Nocht Institute for Tropical Medicine, Zoonoses Group, Bernhard-Nocht-Strasse 74, 20359 Hamburg, Germany.

\*\* Corresponding author at: Bundeswehr Hospital Hamburg, Bernhard-Nocht-Strasse 74, 20359, Hamburg, Germany.

E-mail addresses: [tappe@bnitm.de](mailto:tappe@bnitm.de) (D. Tappe), [Krueger@bnitm.de](mailto:Krueger@bnitm.de) (A. Krüger).

with fatal outcome (Masina and Broady, 1999). Indeed, dozens of Verreaux's sifakas (*Propithecus verreauxi*) infested with large numbers of ticks died in southern Madagascar in 2018 possibly through tick paralysis as indicated by paralyzed limbs prior to apnea (Bittel, 2018; Carver, 2018).

Above all, ectoparasites are of interest as vectors of pathogens (Reeves et al., 2006; de la Fuente et al., 2008; Rakotonanahary et al., 2017). The black rat (*Rattus rattus*) acts as a host for various ectoparasites (Duplantier and Duchemin, 2003a, b; Klompen, 2003), and serves as reservoir of a variety of vector-borne pathogens such as *Yersinia pestis* (Duplantier and Duchemin, 2003a). This is of relevance as black rats are not only associated with humans but also enter natural habitats (Goodman, 1995; Ganzhorn, 2003; Scott et al., 2006). In addition, as a part of the traditional livestock husbandry, cattle are driven over large distances in search for food and water in many parts of Madagascar (Ratvonamana et al., 2013; Feldt and Schlecht, 2016; Goetter, 2016), thereby crossing both degraded and protected areas. The increased contact with the endemic fauna can result in pathogen transmissions between human settlements, cultivated land and pristine habitats.

Apart from the increase in contact zones between humans and wildlife, the degradation of pristine habitat *per se* is assumed to increase parasite loads and susceptibility to diseases in native wildlife, though this may not always be the case (Civitello et al., 2015; Rakotoniaina et al., 2016).

Here, we examine ectoparasites of livestock and endemic Malagasy vertebrates along a gradient of land use ranging from natural forest to agricultural land and villages in the dry south-western part of

Madagascar. Specific questions were: (1) Which ectoparasites are present on different hosts in the area, and which are shared between them, thus providing the chance for the transmission of vector-borne diseases? (2) Does parasite prevalence correlate with habitat disturbance, and does it show seasonal variation? (3) Does transhumance contribute to the spread of ectoparasites?

## 2. Methods

### 2.1. Study site and period

The study was conducted from June to August 2016 (dry season) and from October 2016 to April 2017 (wet season) in south-western Madagascar (Betioky district, Atsimo-Andrefana Region, south of Tulear), at the western edge of the northern part of Tsimanampetsotsa National Park (TNP) and between TNP and the coast (Fig. 1). The region is characterized by irregular rainfall of about 300–350 mm per year and an annual mean temperature of 24 °C (Ratvonamana et al., 2011). The plateau to the east of the coastal zone receives more rain and provides fodder for livestock during the wet season.

Within the spiny forest ecosystem (Moat and Smith, 2007), the degradation categories follow Steffens et al. (2017) and range from intact dry spiny forest in TNP (class 1) to an open anthropogenically altered landscape of cultivated fields with hedges bordering on sparsely vegetated shrubland at the coast (class 3). In between, there are forest fragments and dry spiny forest degraded by wood collection and livestock grazing (class 2). Villages were assigned to class 4 (Fig. 1).

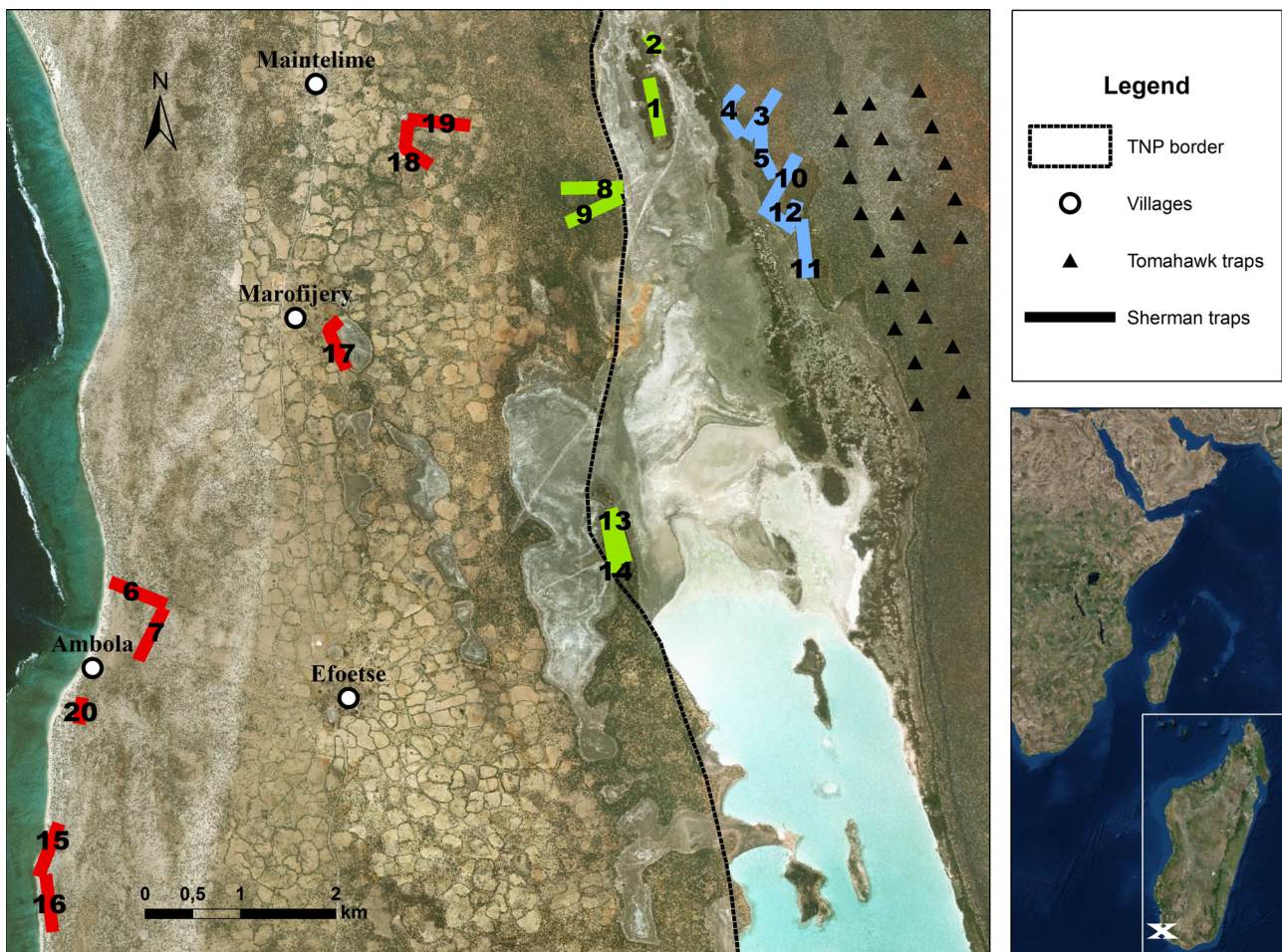


Fig. 1. Map of the study area (littoral) showing locations of Sherman traps line transects (for small mammals, the color indicates the class of habitat degradation: blue = class 1, green = class 2 and red = class 3) and tomahawk traps (for *G. grandieri*) in a grid (Geodetic system: WGS 84, map source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community).

2.2. Sampling of small mammals, lemurs and carnivores

Small mammal including the lemur species *Microcebus griseorufus* were trapped on 20 transects with Sherman live traps (7.7 × 7.7 × 23 cm) along the gradient of degradation (Fig. 1) following standard procedures (Rakotondrany et al., 2010; Bohr et al., 2011). Six transects were installed in habitat classes 1 and 2 each, and another eight transects were set within habitat class 3. Each transect comprised 20 trapping points at 25 m intervals. Two traps were installed at every point: one on the ground and the other one placed in trees or shrubs at a height of 1–2 m. Trapping was carried out for four consecutive nights per transect. Synanthropic rats (*R. rattus*) and mice

(*Mus musculus*) were trapped in huts of the villages Efoetse (E 43.6998, S 24.0786) and Marofijery (E 43.6948, S 24.0427) for two consecutive nights with two Sherman traps in each of ten huts. In the afternoon, traps were baited with banana, and controlled after sunrise the next morning.

The larger endemic carnivore *Galidictis grandidieri* (giant-striped mongoose) was trapped in a grid of tomahawk traps baited with goat skin some 0.5 km east of the line transects within TNP (Fig. 1; for details see Marquardt et al., 2011).

Animals were scanned for ectoparasites using tweezers and a comb. Animals were marked by ear punches to allow identification of recaptures and released at the site of capture. Lemurs were anesthetized

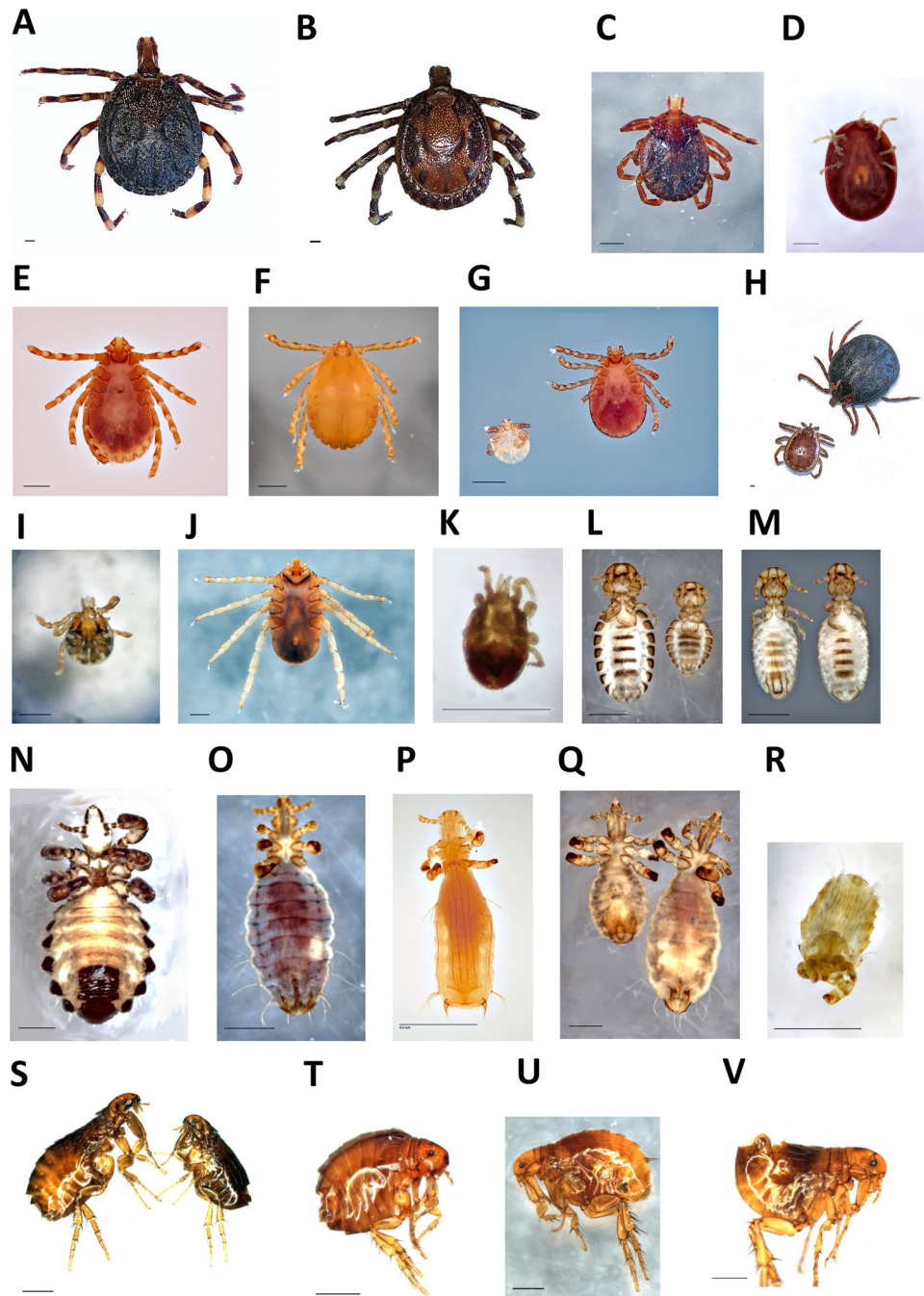


Fig. 2. Plate of images of the different ectoparasite species. Scale bar = 0.5 mm. A–C *A. variegatum*, dorsal view of female, male and nymph. D *A. echinops* nymph. E–G *H. simplex*, female (ventral), male (dorsal), larva and nymph (ventral). H–I *A. chabaudi*, dorsal view of male, female and larva. J female *R. microplus* (ventral). K *O. bacoti*. L *B. caprae*, ventral view of female and male. M ventral view of *B. ovis* male and female. N *H. quadripertusus* male. O *L. africanus* female. P *L. verruculosus* female. Q *L. vituli* male and female. R *H. pacifica*. S *C. felis* male and female. T *E. gallinacea* female. U *X. cheopis* female. V *P. irritans* male.

by i.m. injection of 0.02 ml ketamine 10% (WDT, Garbsen, Germany) (except for lactating females in the rainy season, which were examined at the point of capture and directly released after examination). Rats and mice were sacrificed before examination by cervical dislocation and sprayed with ethanol to immobilize hosted fleas. Disposable gloves were worn during examination. Between examination of different individuals, gloves were changed and instruments were disinfected using ethanol.

### 2.3. Sampling of livestock, pets, poultry and tortoises

Local herders would not allow systematic sampling of their livestock (i.e. goats, sheep and cattle) by foreigners. Therefore, local assistants collected ectoparasites from these animals opportunistically. In order to assess the effects of transhumance, cattle were also sampled on the plateau, where they are moved to for grazing at the beginning of the wet season in December. They are brought back to the littoral in March/April as the littoral provides water year round while the plateau does not (Ratovonamana et al., 2013). We assume that parasite collections from single hosts are incomplete and therefore did not calculate intensities of parasite infestation for livestock.

Small parasite collections from cats, dogs and poultry were received from opportunistic collections from villages conducted by S. J. Rakotondranary. Data from free-ranging tortoises of the study site were taken from Ehlers et al. (2016).

### 2.4. Parasites collection and identification

Ectoparasites were preserved in 2 ml tubes in absolute ethanol. Specimens (except mites) were examined with an Olympus SZ61 stereomicroscope (Olympus Corporation, Shinjuku, Tokyo, Japan) and identified to species based on morphological characteristics (Ward, 1951; Uilenberg et al., 1979; Varma, 1993; Pajot, 2000; Duchemin, 2003; Walker et al., 2014). Mites were mounted after boiling at 122 °C in 85% lactic acid and examined with a Zeiss AxioScope 2 (Carl Zeiss

AG, Jena, Germany). Representative specimens of each parasite species were imaged (Fig. 2) either with integrated cameras (Bresser MicroCam [Bresser Corporation, Rhede, Germany] with Olympus, Nikon Coolpix 950 [Nikon Corporation, Shinagawa, Tokyo, Japan] with Zeiss), or with a custom-made BK Plus Lab System by Dun, Inc. (Palmyra, Virginia, USA) including Canon camera, macro lenses (65 mm and 100 mm), and the BK stacking software.

### 2.5. Statistics

Statistical tests were conducted with R (RCoreTeam, 2018) using RStudio (Version 1.0.44).

## 3. Results

### 3.1. Capture rates and host abundance

Systematic sampling along the 20 transects for small mammals resulted in a total of 6762 trap-nights (Table 1). The insectivorous tenrecs *Echinops telfairi* and *Setifer setosus* are obligatory hibernators and were caught only during the hot wet season (Table 1). Seven individuals of the endemic rodent *Macrotarsomys bastardi* (big footed mouse) were caught in all vegetation types. For this species and the tenrecs sample sizes were too small for statistical analyses. *M. griseorufus* can go into torpor but capture rates did not differ between the wet and the dry season within transects (Wilcoxon matched-pair-signed-rank test:  $W = 27, p = 1, N = 15$  transects where traps were set in both seasons). For *R. rattus* capture rates tended to be higher during the dry than during the wet season (Wilcoxon test:  $W = 20, p = 0.058, N = 15$  transects). In villages rats and mice were also caught in both seasons (Table 1). Apart from the two tenrec species, there was no indication for seasonal differences in the abundance of host species (Table 1). Therefore, seasonal variation in host abundance was not considered in the analyses any further.

**Table 1**  
Transect information for the systematic sampling of small mammals, including *M. griseorufus*.

Transect	Habitat	Habitat class	Dry season					Trap nights	Wet season					
			(June – August 2016)						(Oct. – Dec. 2016 and Feb. – April 2017)					
			<i>Mg</i>	<i>Rr</i>	<i>Mm</i>	<i>Mb</i>	<i>Et/Ss</i>		<i>Mg</i>	<i>Rr</i>	<i>Mm</i>	<i>Mb</i>	<i>Et/Ss</i>	Trap nights
T03	TNP	1	3	0	0	0	0	200	0	0	0	0	0	160
T04	TNP	1	4	0	0	3	0	200	3	0	0	0	0	320
T05	TNP	1	6	0	0	0	0	160	12	0	0	1	0	320
T10	TNP	1	1	2	0	0	0	160	1	1	0	0	0	160
T11	TNP	1	4	0	0	0	0	160	2	0	0	0	0	160
T12	TNP	1	3	0	0	0	0	160	1	0	0	0	0	160
Camp	TNP	1	2	4	0	0	0	50	2	2	0	0	0	60
T01	deg. For.	2	8	4	0	0	0	320	17	2	0	0	0	320
T02	deg. For.	2	0	0	0	0	0	160	6	0	0	0	0	160
T08	deg. For.	2	3	0	0	1	0	160	4	0	0	0	2	160
T09	deg. For.	2	0	1	0	0	0	160	6	0	0	0	0	160
T13	deg. For.	2	1	0	0	0	0	160	–	–	–	–	–	–
T14	deg. For.	2	1	0	0	0	0	160	–	–	–	–	–	–
T17	Fields	3	2	1	0	0	0	160	4	0	0	0	0	320
T18	Fields	3	3	0	0	0	0	160	2	0	0	0	0	320
T19	Fields	3	0	0	0	0	0	160	0	1	0	0	0	328
T06	Shrub	3	0	0	0	1	0	160	–	–	–	–	–	–
T07	Shrub	3	0	0	0	0	0	160	–	–	–	–	–	–
T15	Shrub	3	0	0	0	1	0	160	0	0	0	0	0	160
T16	Shrub	3	0	0	0	0	0	160	–	–	–	–	–	–
T20	Shrub	3	1	0	0	0	0	4	0	1	0	0	1	160
Marofijery	Village	4	0	0	3	0	0	40	0	2	7	0	0	180
Efoetse	Village	4	0	5	8	0	0	40	0	4	17	0	0	180

Numbers are individuals caught without recaptures. Habitat: TNP = Tsimanampetsotsa National Park; deg. For. = degraded forest; Fields = Agricultural fields. Habitat classification ranges from 1 (= intact forest) to 4 (villages). Species abbreviations: Lemurs: *Mg* = *Microcebus griseorufus*; Rodents: *Rr* = *Rattus rattus*; *Mm* = *Mus musculus*; *Mb* = *Macrotarsomys bastardi*; Insectivores: *Et* = *Echinops telfairi*; *Ss* = *Setifer setosus*.

### 3.2. Mammalian ectoparasites

Seventeen different species of ectoparasites were recorded in the study area, infesting a total of 15 host species (Table 2; Fig. 2). These ectoparasites predominantly belong to ticks (Ixodida: Ixodidae and Argasidae), lice (Phthiraptera: Anoplura: Polyplacidae, Linognathidae, Haematopinidae and Hoplopleuridae; Phthiraptera: Ischnocera: Trichodectidae) and fleas (Siphonaptera: Pulicidae). In addition, one species of mesostigmatid mite was found infesting *R. rattus*, which showed morphological characters of the tropical rat mite *Ornithonyssus bacoti*. The five species of ticks were the endemic *Amblyomma chabaudi*, *Haemaphysalis simplex* and *Argas echinops* and the introduced *Amblyomma variegatum* and *Rhipicephalus microplus*. Lice were represented by seven species. The only endemic louse species was *Lemurpediculus verruculosus*, found on *M. griseorufus*. A single individual of *Hoplopleura pacifica* was encountered on *R. rattus*. The remaining five species (sucking lice: *Haematopinus quadripertusus*, *Linognathus vituli*, *L. africanus*; chewing lice: *Bovicola caprae*, *B. ovis*) were all associated with livestock. Four species of fleas included the tropical rat flea *Xenopsylla cheopis* and the cosmopolitan *E. gallinacea*, *Ctenocephalides felis* and *Pulex irritans*.

### 3.3. Ectoparasite species shared between host species

Lice showed a very restricted host spectrum. Five species were found on a single host species. *Bovicola ovis* appeared to be the least host-specific louse, infesting 28% of the sheep and 5% of the goats. *Haematopinus quadripertusus*, regularly infesting cattle (=cattle tail louse), was additionally encountered on one goat. One individual of the cattle tick *R. microplus* was also found on a goat, while two individuals of the endemic rodent *M. bastardi* were infested by one larva of *A. chabaudi*. *Haemaphysalis simplex* infested both tenrec species. The only soft tick species, *A. echinops*, was collected from *E. telfairi*.

Fleas revealed the broadest host spectrum headed by *E. gallinacea* (six host species), which was found on cats, dogs, poultry, rats, mice and the endemic carnivore *G. grandidieri*. *Ctenocephalides felis* was removed from cats and dogs, *X. cheopis* from rats and mice. *Pulex irritans*, the “human flea”, was associated only with chicken (Table 2).

**Table 2**

Sampled hosts (rows) and their ectoparasites (columns) in the study area. Abbreviations: A.c.: *Amblyomma chabaudi* - A.v.: *Amblyomma variegatum* - R.m.: *Rhipicephalus microplus* - H.s.: *Haemaphysalis simplex* - A.e.: *Argas echinops* - Le.v.: *Lemurpediculus verruculosus* - H.q.: *Haematopinus quadripertusus* - Li.v.: *Linognathus vituli* - L.a.: *Linognathus africanus* - H.p.: *Hoplopleura pacifica* - B.c.: *Bovicola caprae* - B.o.: *Bovicola ovis* - E.g.: *Echidnophaga gallinacea* - C.f.: *Ctenocephalides felis* - X.c.: *Xenopsylla cheopis* - P.i.: *Pulex irritans* - O.b.: *Ornithonyssus bacoti*.

		Ticks					Lice					Fleas				Mite		
		A.c.	A.v.	R.m.	H.s.	A.e.	Le.v.	H.q.	Li.v.	L.a.	H.p.	B.c.	B.o.	E.g.	C.f.	X.c.	P.i.	O.b.
Endemic mammals	<i>Microcebus griseorufus</i>							x										
	<i>Macrotarsomys bastardi</i>	x																
	<i>Setifer setosus</i>				x													
	<i>Echinops telfairi</i>				x	x												
	<i>Galidictis grandidieri</i>													x				
Introduced	<i>Rattus rattus</i>									x			x		x			x
	<i>Mus musculus</i>												x		x			
Domestic animals and livestock	Cat*												x	x				
	Dog												x	x				
	Goat				x													
	Sheep							x		x				x				
	Cattle																	
	Chicken*				x	x												
								x	x									
Tortoises	<i>Astrochelys radiata</i> **	x												x			x	
	<i>Pyxis arachnoides</i> **	x																

\* Samples provided by Rakotondranary (unpubl. data).

\*\* Data from Ehlers et al., 2016.

### 3.4. Prevalence of ectoparasites

#### 3.4.1. Habitat disturbance

Except for *M. griseorufus* and *R. rattus*, captures from particular habitats were too low, or restricted to one single habitat (*M. musculus* to villages, *G. grandidieri* to TNP) restraining statistical comparison. In *M. griseorufus*, prevalence of *L. verruculosus* differed significantly between habitats (Fisher’s exact  $p = 0.005$ ). The prevalence in habitat class 3 exceeded the prevalence in habitat class 2 (42% vs. 20%) but was highest in class 1 (52%).

Ectoparasite prevalence (all species) of *R. rattus* was three times higher in villages than in the other habitats. Fleas were only present on rats caught inside houses (*E. gallinacea* and *X. cheopis*: 73% prevalence), and mites occurred on rats in all habitats except villages (Table 3).

#### 3.4.2. Seasonal variation

*Lemurpediculus verruculosus* prevalence on *M. griseorufus* was 52% in the dry and 25% in the wet season ( $\chi^2 = 6.872$ ,  $df = 1$ ,  $p = 0.009$ ,  $N = 102$ ). On rats, neither fleas nor mites showed different prevalence between seasons ( $N = 30$ ; fleas: *E. gallinacea*: Fisher’s exact  $p = 0.70$ ; *X. cheopis*:  $p = 1$ ; mites:  $p = 0.052$ ), although, all rats infested by mites ( $N = 5$ ) were caught in the dry season (Table 4). Flea prevalence of mice did not differ between the two seasons (*E. gallinacea*:  $p = 0.297$ ; *X. cheopis*:  $p = 0.78$ ). *Galidictis* had a significantly higher prevalence in the wet than in the dry season (83% vs. 11%;  $p < 0.001$ ).

#### 3.4.3. Sex bias

No host species showed sexually biased prevalence (*M. griseorufus*:  $\chi^2 = 0.321$ ,  $df = 1$ ,  $p = 0.57$ ,  $N = 83$ ; *R. rattus*:  $\chi^2 = 0.031$ ,  $df = 1$ ,  $p = 0.86$ ,  $N = 25$ ; *M. musculus*: Fisher’s exact  $p = 0.60$ ,  $N = 11$ ; *G. grandidieri*:  $p = 0.31$ ,  $N = 42$ ).

### 3.5. Mean intensity of ectoparasite infestation

#### 3.5.1. Habitat disturbance

Since *L. verruculosus* and the rat mite (*O. bacoti*) were the only parasite species present in several habitats, the analysis of habitat disturbance was limited to these two species (Table 3). The mean intensity of *L. verruculosus* infestation did not differ between habitats (Kruskal-Wallis:  $\chi^2 = 1.924$ ,  $df = 2$ ,  $p = 0.38$ ). The intensity of mite infestation tended to be higher in TNP (3.7 mites per infected host in habitat class 1,

**Table 3**

Variation of ectoparasite infestation along a degradation gradient in the littoral. Classes of habitat degradation are: (1) relatively pristine forest of Tsimanampetsotsa National Park, (2) degraded forest, (3) cultivated and shrub land, (4) villages. (Mean intensities of livestock infestation could not be calculated due to presumed incompleteness of sampling).

Host species Parasite species	Number of individuals				Number of infested hosts / prevalence / mean intensity (range)			
	habitat class 1	2	3	4	habitat class 1	2	3	4
<i>Microcebus griseorufus</i>	44	46	12					
<i>Lemurpediculus verruculosus</i>	89	18	8		23 / 52% / 3.9 (1-25)	9 / 20% / 2 (1-4)	5 / 42% / 1.6 (1-3)	
<i>Macrotarsomys bastardi</i>	4	1	2					
<i>Amblyomma chabaudi</i>			2				2 / 100% / 1	
<i>Setifer setosus</i>		1	1					
<i>Haemaphysalis simplex</i>		11				1 / 100% / 11		
<i>Echinops telfairi</i>		1						
<i>Haemaphysalis simplex</i>		8				1 / 100% / 8		
<i>Argas echinops</i>		12				1 / 100% / 12		
<i>Rattus rattus</i>	9	7	3	11				
<i>Hoplopleura pacifica</i>		1				1 / 14% / 1		
<i>Ornithonyssus bacoti</i>	11	1	1		3 / 33% / 3.7 (1-6)	1 / 14% / 1	1 / 33% / 1	
<i>Echidnophaga gallinacea</i>				146				8 / 73% / 18.3 (2-40)
<i>Xenopsylla cheopis</i>				30				8 / 73% / 3.8 (1-6)
<i>Mus musculus</i>				35				
<i>Echidnophaga gallinacea</i>				46				5 / 14% / 9.2 (2-19)
<i>Xenopsylla cheopis</i>				19				9 / 26% / 2.1 (1-4)
<i>Galidictis grandidieri</i>	50							
<i>Echidnophaga gallinacea</i>	64				14 / 28% / 4.6 (1-14)			
<b>Dog</b>				4				
<i>Ctenocephalides felis</i>				14				4 / 100% / 3.5 (1-7)
<i>Echidnophaga gallinacea</i>				20				3 / 75% / 6.7 (6-7)
<b>Goat</b>				151				
<i>Bovicola caprae</i>				78				24 / 16% / NA
<i>Bovicola ovis</i>				15				8 / 5% / NA
<i>Linognathus africanus</i>				54				13 / 9% / NA
<i>Rhipicephalus microplus</i>				1				1 / 1% / NA
<b>Sheep</b>				130				
<i>Bovicola ovis</i>				133				36 / 28% / NA
<b>Cattle</b>				89				
<i>Haematopinus quadripertusus</i>				37				6 / 7% / NA
<i>Linognathus vituli</i>				102				7 / 8% / NA
<i>Amblyomma variegatum</i>				1				1 / 1% / NA
<i>Rhipicephalus microplus</i>				1				1 / 1% / NA

and 1 mite per infected host in habitat classes 2 and 3), but the number of mite-infested rats was too low for statistical analyses (N = 5). Mean intensities did not show seasonal variation or any sex bias.

3.6. Seasonal prevalence of ectoparasites associated with livestock

Goats, sheep and cattle screened in the vicinity of the trapping transects showed strong seasonal differences especially in the prevalence of lice that were exclusively present in the wet season (Table 4). There was no seasonal variation in ticks infesting cattle, given that only one individual of *R. microplus* had been collected in the wet season (Fisher’s exact p = 1) and a single *A. variegatum* in the dry season (Fisher’s exact p = 0.202).

3.7. Transhumance

The 54 cattle sampled in the littoral between August and November 2016 (N = 18 per month) harbored two ticks, while the same number of ticks was found on only nine cattle on the plateau. The louse species *H. quadripertusus* and *L. vituli* were recorded in October and November with a slightly rising prevalence (October: *H. quadripertusus* 11%; *L. vituli*: 17%; November: 22% each). 238 cattle screened on the plateau in March and April 2017, shortly before transhumance to the littoral and 35 cattle screened in the littoral after having returned from the plateau revealed a pronounced difference in tick prevalence (Fisher’s exact p = < 0.001, N = 273). *Amblyomma variegatum* was present on 6%, and *R. microplus* on 24% of the cattle grazing on the plateau. The cattle herd in the littoral was tick-free.

4. Discussion

This study reports ectoparasites on mammals, poultry and tortoises in south-western Madagascar. Screening of 15 endemic and domestic host species revealed 17 different species of ticks, lice, fleas and mites. *M. griseorufus* was the host species caught most frequently by systematic trapping. The sucking louse *L. verruculosus* occurred on 36% of 102 host individuals. Yet, none of these individuals was infested by ticks. The ectoparasites of the small nocturnal lemurs, as *Microcebus* spp., have recently been reviewed by Zohdy and Durden (2016). Studies have found *Microcebus* spp. to host the tick species *Ixodes lemuris*, *Haemaphysalis lemuris* and possibly *H. simplex* (Rodriguez et al., 2012; Blanco et al., 2013). Klein et al. (2018) proposed a third *Haemaphysalis* species named “*Candidatus Haemaphysalis microcebi*”. At the Beza Mahafaly Special Reserve (BMSR), some 100 km northeast of our study site, *M. griseorufus* was commonly infested by ticks (74 out of 249 individuals, Rodriguez et al., 2012). In addition, ring-tailed lemurs (*Lemur catta*) are serving as hosts for *H. lemuris* at BMSR (Loudon et al., 2006), but not at TNP (Dutton et al., 2003).

Two species of sucking lice are known to parasitize *Microcebus* spp., both belonging to the genus *Lemurpediculus*. The first described species of this genus was *L. verruculosus*, found on an unspecified “mouse lemur” in the surroundings of Fort Dauphin (Ward, 1951, then *Lemurphytirus verruculosus*). The next record of *L. verruculosus* was from brown mouse lemurs (*Microcebus rufus*) in Ranomafana (Durden et al., 2010). An individual louse identified tentatively as *L. verruculosus* was recovered from *M. griseorufus* at the BMSR (Rodriguez et al., 2012). With our louse collection we now confirm that *M. griseorufus* is another host of this

**Table 4**  
Seasonal variation of ectoparasite infestation.

Host species	Number of individuals		Number of infested hosts/ prevalence/mean intensity (range)	
	dry	wet	dry	wet
<b>Parasite species</b>				
<i>Microcebus griseorufus</i>	42	60		
<i>Lemurpediculus verruculosus</i>	41	74	22 / 52% / 1.9 (1-3)	15 / 25% / 4.9 (1-25)
<i>Macrotarsomys bastardi</i>	6	1		
<i>Amblyomma chabaudi</i>	2		2 / 33% / 1	
<i>Setifer setosus</i>		2		
<i>Haemaphysalis simplex</i>		11		1 / 50% / 11
<i>Echinops telfairi</i>		1		
<i>Haemaphysalis simplex</i>		8		1 / 100% / 8
<i>Argas echinops</i>		12		1 / 100% / 12
<i>Rattus rattus</i>	17	13		
<i>Hoplopleura pacifica</i>		1		1 / 8% / 1
<i>Ornithonyssus bacoti</i>	13		5 / 29% / 2.6 (1-6)	
<i>Echidnophaga gallinacea</i>	61	85	4 / 23% / 15.2 (6-24)	4 / 31% / 21.3 (2-40)
<i>Xenopsylla cheopis</i>	17	13	5 / 29% / 3.4 (1-6)	3 / 23% / 4.3 (2-6)
<i>Mus musculus</i>	11	24		
<i>Echidnophaga gallinacea</i>	41	5	3 / 27% / 13.7 (8-19)	2 / 8% / 2.5 (2-3)
<i>Xenopsylla cheopis</i>	3	16	2 / 18% / 1.5 (1-2)	7 / 29% / 2.3 (1-4)
<i>Galidictis grandidieri</i>	38	12		
<i>Echidnophaga gallinacea</i>	20	77	4 / 10% / 5 (1-8)	10 / 83% / 7.7(3-14)
<b>Dog</b>		4		
<i>Ctenocephalides felis</i>		14		4 / 100% / 3.5 (1-7)
<i>Echidnophaga gallinacea</i>		20		3 / 75% / 6.7 (6-7)
<b>Goat</b>	23	128		
<i>Bovicola caprae</i>		78		24 / 19% / NA
<i>Bovicola ovis</i>		15		8 / 6% / NA
<i>Linognathus africanus</i>		54		13 / 10% / NA
<i>Rhipicephalus microplus</i>	1		1 / 4% / NA	
<b>Sheep</b>	14	116		
<i>Bovicola ovis</i>		133		36 / 31% / NA
<b>Cattle</b>	18	71		
<i>Haematopinus quadripertusus</i>		37		6 / 8% / NA
<i>Linognathus vituli</i>		102		7 / 10% / NA
<i>Amblyomma variegatum</i>	1		1 / 6% / NA	
<i>Rhipicephalus microplus</i>		1		1 / 1% / NA

Mean intensities of livestock infestation could not be calculated (=NA) due to presumed incompleteness of sampling. Opportunistically sampled cats and chicken are excluded.

louse species and suggest that *L. verruculosus* is indeed less host specific than thought.

The endemic rodent *M. bastardi* is rarely trapped by our trapping procedure (Ganzhorn, 2003; Youssouf and Rasoazanabary, 2008). It had never been trapped in the study area before during ten years of trapping. Two individuals were infested with *A. chabaudi* larvae while adult *A. chabaudi* are known from the endemic tortoises (Ehlers et al., 2016). Only a few *Haemaphysalis* ticks have been associated with *M. bastardi* in the past (Uilenberg et al., 1979). Here we present the first record of *A. chabaudi* infesting the rodent *M. bastardi*. So far, this tick has been considered as a strictly host specific tortoise tick.

The two tenrec species *S. setosus* and *E. telfairi* are the preferred hosts of *H. simplex*, but Uilenberg et al. (1979) reported this tick also from *Tenrec ecaudatus*, *M. bastardi* and in rats' nests. It had also been recovered from lemurs, the sifaka *Propithecus verreauxi*, probably an accidental host (Uilenberg et al., 1979), and *M. griseorufus*, where it could be more common (Rodriguez et al., 2012). In the TNP region we found *H. simplex* on the two tenrec species, but dissenting from the

literature (Hoogstraal and Kim, 1985) we encountered this tick species among the tenrecs' body spurs, not in the ears. *Haemaphysalis simplex* was neither associated with rodents (N = 6 *M. bastardi* and N = 19 *R. rattus*) nor with mouse lemurs.

Rats receive special attention in Madagascar due to the repeated emergence of plague. Two species of fleas are involved in plague circulation: *X. cheopis*, which was introduced together with its host, and the endemic *Synopsyllus fonquerniei*. The latter is known from rats living outside human settlements. This is important for possible sylvatic plague cycles and suspected transmission to endemic rodents with consequent die-off (Duplantier and Duchemin, 2003a, b; Duplantier et al., 2005). In contrast, *X. cheopis* generally infests rats inside houses (Duplantier and Duchemin, 2003a) as also observed in the present study. Eight out of 11 rats (73%) caught in houses were infested by *X. cheopis*. The same proportion was found hosting a second flea species, the sticktight flea (*E. gallinacea*). We also observed mice serving as hosts for both flea species. The coexistence of mice could be an important factor in maintaining flea populations. *Paractenopsyllus* represents another genus of fleas known to parasitize *R. rattus* (Duchemin, 2003; Hastriter and Dick, 2009). This genus was reported to be predominantly hosted by shrew tenrecs (*Microgale*) and rodents of the genus *Eliurus* from rain forests of the central highlands or the northern mountains of Madagascar (Duchemin, 2004; Hastriter and Dick, 2009). Consistently, we did not find *Paractenopsyllus* fleas at our study site, where most main hosts are absent (except *Eliurus myoxinus*, Soarimalala and Goodman, 2011) and the climate is much drier.

Apart from fleas, O'Connor et al. (2003) listed five species of mites infesting rats, and seven tick species have been recovered from rats across the country (Uilenberg et al., 1979). It thus seems prudent to suggest that rats are suitable vehicles for transmission of further ectoparasite species between mammalian hosts. Nevertheless, the free-ranging rats trapped at TNP did not reveal any ectoparasites except for mesostigmatid mites, which have not been found on any other host (Table 2). Laelapid mites were seen on 17 out of 20 *L. catta* at TNP (Dutton et al., 2003). In BMSR even all *L. catta* individuals had mesostigmatid mites (Loudon et al., 2006). However, due to uncertain identification of mites, it remains unclear if *L. catta* from different regions share the same species of parasitic mite.

*Galidictis grandidieri* was infested by introduced *E. gallinacea* fleas. No record of ectoparasites has been published or deposited in the Global Mammal Parasite Database (GMPD, [www.mammalparasites.org](http://www.mammalparasites.org); Nunn and Altizer, 2005). Since *G. grandidieri* occurs from the original forest to the vicinity of human settlements (Marquard et al., 2011), it could easily be infected by fleas when feeding on leftovers of chicken, infested by *E. gallinacea*. *Echidnophaga gallinacea* is not known as a vector for specific diseases but can cause severe skin irritations and a general decline in health. No such signs were noted in *G. grandidieri*.

#### 4.1. Habitat disturbance

Habitat disturbance is supposed to correlate positively with ectoparasite prevalence (Wright et al., 2009; Junge et al., 2011) due to nutritional stress and consequently impaired immune functions or due to reduced biodiversity (Beck and Levander, 2000; Chapman et al., 2005; Irwin et al., 2010; Civitello et al., 2015). The infestation of the endemic *G. grandidieri* by an introduced parasite species demonstrates an undeniable anthropogenic effect. Yet, only *M. griseorufus* was caught in sufficient numbers throughout the different habitats to allow statistical comparison. The mean intensity of louse infestation did not differ between the habitats. The prevalence of louse infestation, however, was notably higher in the habitat of degradation class 3 (42%) than in the second most degraded habitat (20%), but it was even higher in TNP (52%). This result contrasts with the assumption that habitat degradation leads to higher ectoparasite prevalence. This finding is inconsistent with the "biodiversity dilution effect" that postulates decreased loads of host-specific parasites with increasing number of

species (Civitello et al., 2015). Thus, other (or additional) ecological characters overwrite the possible effects of habitat quality and contacts by livestock and domestic animals. Possible candidates are increased social contacts due to higher population densities in pristine than in degraded habitats (Kappeler et al., 2015; Nunn et al., 2015).

#### 4.2. Other impacts

Host density, for example, is crucial for survival of ectoparasite populations. A higher host density would mean a higher possibility for the parasite to find a suitable host (in the case of a tick). And it would also increase the chance of the parasite to actively change the host or to be transmitted from one host to another given that host individuals from dense populations more often encounter conspecifics. It is true that, by offering stable food resources, habitat quality favors population density (Balko and Underwood, 2005), but, on the other hand, this can also be mediated by habitat loss or fragmentation. In a shrinking habitat the density of inhabiting populations would rise, at least initially (Debinski and Holt, 2000). Both could be valid for our case. Nevertheless the density proxy of mouse lemurs we calculated (animal captures per 100 trap nights) rises with habitat quality (from habitat class 3 to 1: 2.5, 3.5, 3.8), which could illustrate the higher prevalence in the pristine forest following a higher density, but giving no explanation for the interrupting decline of prevalence in habitat class 2.

There are also conceivable behavioral aspects influencing prevalence and intensity of infestation with ectoparasites. Grooming is an important social activity in primates to reduce ectoparasite loads (Hutchins and Barash, 1976; Akinyi et al., 2013). Nevertheless, lemurs are not able to use their hands or lips for grooming like higher primates, but use their "tooth comb" to groom themselves or group members (Sauther et al., 2002). In consequence some body parts like the face, head, neck and parts of the upper back are inaccessible for auto-grooming lemurs (Hutchins and Barash, 1976), so that they depend on allogrooming in social relationships to clean these regions from ectoparasites. This situation means a disadvantage for solitary individuals.

Recent studies have also shown that sleeping ecology may have an impact on parasite infestation (Hokan et al., 2017; Klein et al., 2018). Hence, sleeping in tree holes apparently increases infestation with mites, lice and ticks, and sleeping in groups promotes the infestation with lice. While these studies and our study on pair-living or solitary species found independency of ectoparasite prevalence from host gender, males of the multi-male multi-female group living *Lemur catta* in BMSR hosted more mites (Sauther et al., 2006) and more ticks and lice than females (Sauther et al., 2002).

#### 4.3. Seasonal effects

Ectoparasite prevalence and intensity are assumed to be higher during the wet season, when environmental conditions are favorable for parasite survival (Altizer et al., 2006). The louse infestation of the sheep and goats in the littoral of our study site matches this assumption. Yet, we also observed a strong - albeit reverse - seasonal pattern in louse infestation of *M. griseorufus*. Half of the lemurs trapped in the dry season was infested by *L. verruculosus*, compared to only a quarter of individuals being infested in the wet season. In Ankarafantsika National Park louse prevalence of mouse lemurs was also higher in the dry season, with a peak at its end in October (up to 90%, Klein et al., 2018). However, the prevalence was very variable between years with 3% in May 2015 at the beginning of the dry season, and 74% in May 2016. Other regions or hosts showed a seasonal peak of louse infestation towards the wet season (Wright et al., 2009; Hokan et al., 2017).

At BMSR immature stages of *H. lemuris* have been found on *M. griseorufus* only in the dry season (Rodriguez et al., 2015), whereas adult ticks infest sifakas and ring-tailed lemurs year-round (Loudon et al., 2006). As humidity is claimed to be the most limiting factor for tick survival because of their susceptibility to desiccation (Needham

and Teel, 1991; Gray et al., 2009), ticks might reach their distribution limit between the Mahafaly Plateau and the littoral due to decreasing rainfall and humidity.

#### 4.4. Ectoparasites of livestock

The six ectoparasite species encountered on livestock are well known in Africa and other tropical regions (Durden and Musser, 1994; Walker et al., 2014), indicating that they have been introduced to Madagascar in the course of livestock trade (Uilenberg, 1964). It is surprising that merely such a small number of livestock-associated ectoparasites had managed to settle in Madagascar. From the some 20 species of ixodid ticks infesting livestock under similar climatic conditions in southern and eastern Africa (Walker et al., 2014), only *A. variegatum* and *R. microplus* have spread to the island. The latter is supposed to have its origin in Southeast Asia, while *A. variegatum* originates from east Africa (Barré and Uilenberg, 2010).

Occurrence of ticks on livestock is affected by seasonality and strongly depends on the tick's life stage (Yawa et al., 2018). A study from Gambia reports that adult *A. variegatum* infest cattle in the rainy season, and almost disappear in the dry season (Mattioli et al., 1997). In Africa this species occupies all climatic zones, and is supposed to be limited only by arid conditions, i.e. below 400 mm annual rainfall, like in the Sahel (Barré and Uilenberg, 2010). The virtual absence of ticks in the littoral of our study site may also be due to aridity. This observation is consistent with reports by local stockbreeders who claim that cattle are in better health condition in the littoral compared to the plateau.

Lice of livestock were exclusively present in the hot rainy season - a special case, as it is known that louse survival and development is limited by temperature (Matthysse, 1944) and that louse populations of livestock decline in the hottest months in tropical regions and peak in the cold, dry season (Gabaj et al., 1993; Kumar et al., 1994; Rashmi and Saxena, 2017). However, we cannot exclude that our observation is biased by insufficient sampling in the dry season.

### 5. Conclusion

This study provides confirmation of a broad spectrum of ectoparasites being present in the examined area. Most ectoparasites found in this study were rather host-specific providing little potential for inter-specific disease transmission. Yet, black rats, cats and dogs can transport *E. gallinacea* fleas into the forest where they can infect endemic carnivores and vice versa. Seasonal or habitat effects were tested significant for louse infestation of *M. griseorufus*. In contrast to most other studies, the prevalence was highest in the least degraded habitat and showed an increase towards the dry season. Yet, as no further predictors have been recorded, we only can discuss the reasons.

We demonstrated that transhumance of cattle towards the drier littoral possibly diminishes tick burdens of a herd.

#### Declarations of interest

None.

#### Ethical approval

All applicable institutional and/or national guidelines for the care and use of animals were followed. Fieldwork was authorized by the Ministère de L'Environnement, de l'Ecologie, de la Mer et des Forêts. (Research permits: No 136/16/- and No 002/17/MEEF/SG/ DGF/DSAP/SCB.Re; export permit: No 345-17/MEEF/SG/DGF/ DREEFA-AND/SFR). This article does not contain any studies with human participants performed by any of the authors.



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