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BLOOD PARASITES IN BIRDS FROM MADAGASCAR

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ABSTRACT: Madagascar has long been recognized for its unique and diverse biota. In particular, significant effort has been made to establish baseline population data to better conserve the endemic avifauna. During field expeditions between 1993 and 2004, birds were mist-netted at 11 different sites, at elevations from 60 m to 2,050 m above sea level. Data on endemic status, forest type, and habitat preference were recorded. Thin blood films from 947 birds, belonging to 26 families and 64 species, were examined by light microscopy to determine the prevalence of blood parasites. Of these 947 birds, 30.7% were infected by at least one species of blood parasite, 26.8% of which were infected by more than one species. Species of *Haemoproteus* were the most prevalent (17.4%), followed by microfilariae (11.0%), *Leucocytozoon* spp. (9.4%), *Plasmodium* spp. (1.9%), *Trypanosoma* spp. (0.9%), and *Babesia* spp. (0.2%). Species level identifications confirmed the presence of 47 species of hemosporidians and trypanosomes, which is notably high and mirrors the diversity of their avian hosts. Eleven (23.4%) of these parasite species were new to science and thought to be endemic to the island. Significant differences in prevalence were observed by sample site, forest type (humid vs. dry), and habitat preference. Birds from all elevational zones sampled were infected, although not all parasite genera were present in each zone. Four of the six endemic avian families or subfamilies (Bernieridae, Brachypteraciidae, Philepittinae [Eurylaimidae], and Vangidae) were sampled and found to be parasitized. Of the families with the largest sample sizes, the Zosteropidae and Ploceidae had the highest prevalence of infection (65.6% and 49.3%, respectively). The vectors of hematozoan parasites in Madagascar are currently unknown. These results add to the current knowledge of avian parasitism in Madagascar and are of particular interest for the conservation of endemic species, as well as threatened or endangered populations.

Key words: Avian, conservation, Hematozoa, *Haemoproteus*, *Leucocytozoon*, Madagascar, *Plasmodium*, *Trypanosoma*.

INTRODUCTION

The flora and fauna of Madagascar boast an extraordinary level of endemism, and new species of higher taxa are being reported regularly (Goodman and Benstead, 2005). Of the 283 species of birds found in Madagascar, 209 are known to be breeding residents. Just over half of these 209 are endemic (Hawkins and Goodman, 2003), and there are 37 endemic genera, the majority of which are forest dwelling.

Three previous investigations of blood parasites infecting Malagasy birds have been published. Bennett and Blancou (1974) examined 64 birds representing 32 species and found 14 individuals (representing eight species) to be infected. This preliminary study concluded that the prevalence of blood parasites was low, and there were no apparent island-endemic species of hematozoa. The second study examined smears from 10 birds (Greiner et al., 1996) among which six had blood parasites, and this study reported mixed infections in Malagasy birds for the first time. Most recently, Raharimanga et al. (2002) published a study of hematozoa of Malagasy birds from six locations, but no information was presented on the specific identity of the parasites, which pre-empts a certain level of analysis. As a result of the current survey, which includes a re-evaluation of all material used by Raharimanga et al. (2002), we have been able to identify many of the parasites present in a broad sample.

The goal of the current study was to obtain a broad perspective on the distribution of avian hematozoa across different areas of Madagascar. In addition, we attempted to identify other factors, such as elevation, forest type, or habitat preference, that might be associated with parasite transmission on the island.

MATERIALS AND METHODS

Over repeated field expeditions between 1993 and 2004, ornithologists mist-netted birds at numerous sites in both dry (less than 1 m of annual rainfall) and humid (greater than 1.5 m of annual rainfall) forests across Madagascar. These sites are, from north to south (Fig. 1), Montagne d'Ambre (humid forest, 12°32′S, 49°10′E, 1,000 m), Marojejy (humid forest, 14°25.6′S, 49°36.5′E, 450–1,875 m), Anjanaharibe-Sud (humid forest, 14°44.8′S, 49°26.0′E, 875–1,950 m), Namoroka (dry forest, 16°24′S, 45°18′E, 200 m), Ambohitantely (humid forest, 18°10′S, 47°17′E, 1,400–1,500 m), Andranomay (humid forest, 18°28′S, 47°57′E, 1,300 m), Bemaraha (dry forest, 19°08.4′S, 44°49.7′E, 100 m), Ankaratra (humid forest, 19°18′S, 47°14′E, 2,000 m), Andringitra (humid forest, 22°13′S, 47°1′E, 2,050 m), Morombe [=Mikea Forest] (dry forest, 22°47S, 43°31′E, 60–80 m), and Andohahela (humid forest, 24°37.6′S, 46°45.9′E, 400–1,875 m). Samples were pooled into elevational ranges for data analysis. Four-paneled mist-nets measuring 12×2.4 m with 36-mm mesh were installed in the forest understory, with the bottom rung of the net touching or nearly touching the ground. Thus, the majority of species captured and sampled are those that live in, or descend to, the understory.

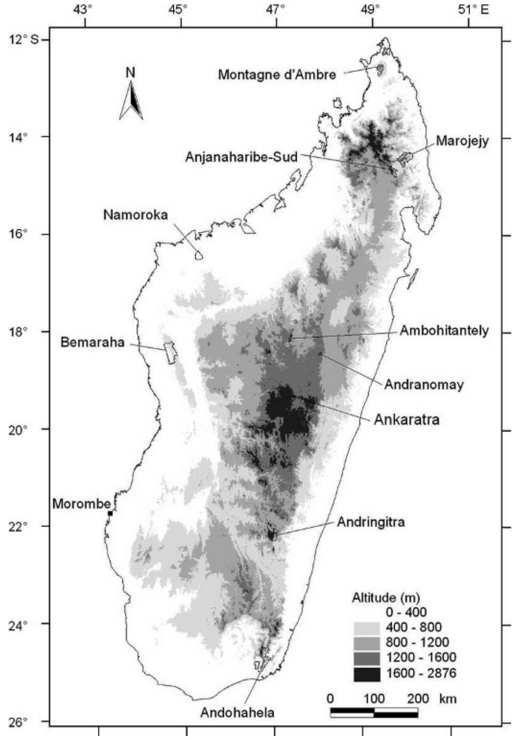

FIGURE 1. Map of Madagascar. Sampling sites are indicated, and altitudinal ranges are shown.

Avian taxonomy follows studies on the phylogenetic relationships of Malagasy birds (Prum, 1993; Cibois et al., 2001; Kirchman et al., 2001; Yamagishi et al., 2001; Schulenberg, 2003; Marks and Willard, 2005; Moyle et al., 2006). Data regarding habitat preference and forest type were recorded by field researchers. Birds were classified as endemic to the region (Madagascar and nearby western Indian Ocean islands), nonendemic, and migratory. Birds were categorized as having one of three habitat preferences and largely following Wilmé (1996): forest-dependant species (FDepS), those that probably never cross an open or nonforested area; forest-dwelling species (FDweS), those that occur within relatively intact forest, at the ecotone between anthropogenic savannah and forest habitats, and are presumed to cross open areas; and forest-edge species (FEdgS), those that live at the boundary between forest and anthropogenic savannah habitats and cross open areas.

Blood was obtained in the field by toe clips (released individuals) or heart puncture (collected voucher specimens part of inventory survey) and then dropped onto a clean glass slide and spread into a monolayer using a second slide. Slides were air-dried, and most were fixed in absolute methanol; some slides were stained with Giemsa before shipment to the Department of Infectious Diseases and

Pathology, College of Veterinary Medicine, University of Florida, Gainesville, Florida, USA. On arrival, the unprocessed slides were fixed in methanol for 30 min and air-dried. Then, slides were stained in 10% Giemsa for 30 min, rinsed with distilled water, and air-dried. Slides were examined on a Zeiss light microscope at 100×, 160×, 400×, and 1,000× (oil immersion) for the presence of hematozoa. Due to varying quality of the smears, slides were examined for 30 min before being declared free of parasites. Parasites were identified using standard morphologic characters in comparison with species reported previously from the same host family, according to the most current available checklists (Bennett et al., 1994; Peirce, 2005) and keys (Valkiunas, 2004). Voucher specimens were submitted to the International Reference Centre for Avian Hematozoa, South Brisbane, Queensland, Australia, accession numbers G465171–G465209. All statistical comparisons were made with SAS 9.1 (SAS Institute, 2003), using a chi-square test to compare prevalence. Analysis of unbalanced sample sizes compared for habitat preference and endemism were repeated using Fisher's exact tests, which did not change the results. Unless otherwise indicated, $\alpha=0.05$.

RESULTS

Of the 947 birds sampled in this survey, composed of 26 families and 64 species, 30.7% (291) were infected with at least one species of hematozoa (Table 1). Species of *Haemoproteus* were the most prevalent (17.4%). Microfilariae were observed in 11.0% of birds, followed by *Leucocytozoon* spp. (9.4%), *Plasmodium* spp. (1.9%), *Trypanosoma* spp. (0.9%), and *Babesia* spp. (0.2%). Multiple infections, defined as infections with more than one type of hematozoan parasite, were observed in 26.8% (78/291) of the infected individuals, or 8.2% (78/947) of all birds sampled. Of the parasites that were identifiable to the species level, there were 25 species of *Haemoproteus*, 15 species of *Leucocytozoon*, five species of *Plasmodium*, and two species of *Trypanosoma* (Table 2). Eleven of these parasite species were previously unrecognized to science and are currently only known from Madagascar. The new species of parasites were reported from three endemic avian families or subfamilies (Brachypteraciidae, Vangidae, and Philepittinae [Eurylaimidae]) and two cosmopolitan families (Dicruridae and Sylviidae) (Savage, 2004; Savage et al., 2004, 2005, 2006a, b; Savage and Greiner, 2004, 2005). The names and prevalence of these new species are as follows: *Haemoproteus forresteri*, 43% (6/14; Brachypteraciidae); *Haemoproteus goodmani*, 14% (2/14; Brachypteraciidae); *Haemoproteus khani*, 78% (11/18; Dicruridae); *Haemoproteus madagascariensis*, 1% (1/91; Vangidae); *Haemoproteus vangii*, 9% (8/91; Vangidae); *Leucocytozoon atkinsoni*, 2% (1/47; Sylviidae); *Leucocytozoan frascai*, 50% (7/14; Brachypteraciidae); *Leucocytozoon greineri*, 18% (14/77; Eurylaimidae); *Leucocytozoon lairdi*, 6% (5/91; Vangidae); *Leucocytozoon vangis*, 3% (3/91; Vangidae); and *Plasmodium parvulum*, 4% (4/91; Vangidae).

Birds from 10 orders and 26 families are represented in this survey (Table 1). Parasites were observed in all families in which more than one bird was sampled. Of the five families in which only one bird was sampled (Campephagidae, Leptosomidae, Rallidae, Threskiornithidae, and Upupidae), none were found to be infected. Species not found to be infected, by family, are as follows (number of individuals examined noted): Accipitridae: *Accipiter madagascariensis* (2), *Milvus migrans* (1); Bernieridae: *Crossleyia xanthophrys* (4), *Hartertula flavoviridis* (1), *Thamnornis chloropetoides* (3); Campephagidae: *Coracina cinerea* (1); Caprimulgidae: *Caprimulgus madagascariensis* (2); Hirundinidae: *Riparia paludicola* (1); Leptosomidae: *Leptosomus discolor* (1); Eurylaimidae: *Neodrepanis hypoxantha* (5); Rallidae: *Canirallus kioloides* (1); Sylviidae: *Acrocephalus newtoni* (1); Threskiornithidae: *Lophotibis cristata* (1); Turdidae: *Saxicola torquata* (7); Vangidae: *Calicalicus madagascariensis* (2), *Newtonia archboldi* (2), *Xenopirostris xenopirostris* (1); and Upupidae: *Upupa marginata* (1). Of families with greater than one individual

TABLE 1. Avian species infected with hematozoa out of the total number of representatives for that species, presented alphabetically by family. The number of infected birds by parasite genera observed also is presented.

Infected species, by host family	No. infected/sampled	Parasite[a]					
		P	H	L	Mf.	T	B
ACCIPITRIDAE							
Accipiter francesii	10/12	1		9			
ALCEDINIDAE							
Alcedo vintsioides	1/9		1		1		
Corythornis madagascariensis	4/16		1		3		
BERNIERIDAE							
Bernieria madagascariensis	15/55		4	2	9	1	
Oxylabes madagascariensis	5/30				5		
Xanthomixis cinereiceps	1/27			1			
Xanthomixis zosterops	4/58			1	3		
BRACHYPTERACIIDAE							
Atelornis crossleyi	5/5		4	2	1	1	
Atelornis pittoides	4/6		4	2		1	
Brachypteracias leptosomus	2/2		1	2	1		
Geobiastes squamigera	1/1			1	1		
CAPRIMULGIDAE							
Caprimulgus enarratus	1/3		1				
COLUMBIDAE							
Streptopelia picturata	4/8		4				
CUCULIDAE							
Coua cristata	2/2			1	2		
Cuculus rochii[b]	1/2				1		
DICRURIDAE							
Dicrurus forficatus	14/18		11		8		
EURYLAIMIDAE							
Neodrepanis coruscans	1/9			1			
Philepitta castanea	17/61			13	9		
Philepitta schlegeli	1/2				1		
HIRUNDINIDAE							
Phedina borbonica	1/1		1		1		
MONARCHIDAE							
Terpsiphone mutata	5/90		3				2
MOTACILLIDAE							
Motacilla flaviventris	4/5		2		1	1	
NECTARINIIDAE							
Nectarinia notata	1/2		1	1			
Nectarinia souimanga	8/24		7	1			
PLOCEIDAE							
Foudia madagascariensis	6/14	1	1	2	2		
Foudia omissa	12/49		8	6	1		
Ploceus nelicourvi	5/19			4	1		
Ploceus sakalava	51/68	2	48	4	12	1	

Table 1. Continued.

Infected species, by host family	No. infected/sampled	Parasite[a] P	H	L	Mf.	T	B
PYCNONOTIDAE							
Hypsipetes madagascariensis[b]	10/33	2	2	5	4		
STRIGIDAE							
Otus rutilus	13/18		12	3	5		
SYLVIIDAE							
Dromaeocercus brunneus	1/1				1		
Neomixis striatigula	3/4		3		1		
Neomixis tenella	1/2		1	1			
Nesillas typica	6/39		5	1			
TURDIDAE							
Copsychus albospecularis	13/59	2	3		9		
Monticola sharpei	12/35	3	8	1	3		
TURNICIDAE							
Turnix nigricollis	1/3				1		
VANGIDAE							
Cyanolanius madagascarinus	1/1		1	1	1	1	
Euryceros prevostii	2/3			2	1		
Falculea palliata	2/5	2	1				
Leptopterus viridis	1/1		1	1			
Mystacornis crossleyi	1/2				1		
Newtonia amphichroa	2/18		2		1		
Newtonia brunneicauda	7/46	2	4		3		
Schetba rufa	1/1	1		1		1	
Tylas eduardi	2/2	1		1	2	1	
Vanga curvirostris	5/7	1	4	2	3		
ZOSTEROPIDAE							
Zosterops maderaspatana	21/32		16	17	1		

[a] P = *Plasmodium* spp.; H = *Haemoproteus* spp.; L = *Leucocytozoon* spp.; Mf. = Microfilariae; T = *Trypanosoma* spp.; B = *Babesia* spp.; MI = multiple infection.

[b] Species not endemic to Madagascar or nearby western Indian Ocean islands.

sampled, prevalence ranged from 6% in the Old World flycatchers (Monarchidae) to 88% in the ground-rollers (Brachypteraciidae). Nine families of birds were represented by at least 30 birds and up to 178. Of these, the two families with the highest prevalence were the Zosteropidae, 66% (21/32) and Ploceidae, 49.3% (74/150). At the species level, 23 of the 64 species sampled had 10 or more individuals examined. Infection prevalence in these 23 species ranged from 6% in *Terpsiphone mutata* to 83% in *Accipiter francesii* (Table 1). Other species with high prevalence of hematozoan infection were *Dicrurus forficatus* (78%), *Ploceus sakalava* (75%), *Otus rutilus* (72%), and *Zosterops maderaspatana* (66%). The majority of birds sampled (903) were endemic to Madagascar, with some also known to occur in the nearby Comoro Islands (Table 1). Forty-two individuals represented nonendemic species, and two birds represented Malagasy endemic breeding species that migrate to Africa during the nonreproductive season. Prevalence of parasitism was 31.0% (280/903) in endemic birds and 24% (10/42) in nonendemic birds. One of two migratory endemic breeding species, *Cuculus rochii*, was

TABLE 2. Parasite species identified from avian host species.

Host species, by family	Parasite species identified
ACCIPITRIDAE	
Accipiter francesii	*Leucocytozoon toddi*, *Plasmodium vaughni*
ALCEDINIDAE	
Alcedo vintsioides	*Haemoproteus fusca*
Ispidina madagascariensis	*H. halyconis*
BRACHYPTERACIIDAE	
Atelornis crossleyi	*H. forresteri*, *L. frascai*
Atelornis pittoides	*H. forresteri*, *H. goodmani*, *L. frascai*, *Trypanosoma avium*
Brachypteracias leptosomus	*H. forresteri*, *L. frascai*
Geobiastes squamigerus	*L. frascai*
CAPRIMULGIDAE	
Caprimulgus enarratus	*H. caprimulgi*
COLUMBIDAE	
Streptopelia picturata	*H. columbidae*
CUCULIDAE	
Coua cristata	*L. centropi*
DICRURIDAE	
Dicrurus forficatus	*H. dicruri*, *H. khani*
EURYLAIMIDAE	
Neodrepanis coruscans	*L. greineri*
Philepitta castanea	*L. greineri*
HIRUNDINIDAE	
Phedina borbonica	*H. prognei*
MOTACILLIDAE	
Motacilla flaviventris	*H. anthi*
TURDIDAE	
Copsychus albospecularis	*H. fallisi*, *H. minutus*, *P. rouxi*
Monticola sharpei	*H. fallisi*, *H. minutus*, *L. majoris*, *P. vaughni*
Nectarinia notata	*H. sequeirae*, *L. nectariniae*
Nectarinia souimanga	*H. sequeirae*, *L. nectariniae*
PLOCEIDAE	
Foudia madagascariensis	*H. quelea*, *P. nucleophilum*, *P. relictum*
Foudia omissa	*H. quelea*, *L. bouffardi*
Ploceus nelicourvi	*L. bouffardi*
Ploceus sakalava	*H. quelea*, *L. bouffardi*, *P. rouxi*, *T. everetti*
PYCNONOTIDAE	
Hypsipetes madagascariensis	*H. philippinesis*, *H. sanguinis*, *L. brimonti*, *L. pycnonoti*, *P. rouxi*
STRIGIDAE	
Otus rutilus	*H. noctuae*, *H. syrnii*, *L. danilewskyi*
SYLVIIDAE	
Neomixis striatigula	*H. wenyoni*
Neomixis tenella	*H. belopolskyi*, *L. atkinsoni*
Nesillas typica	*H. fringillae*, *H. wenyoni*, *L. phylloscopus*
VANGIDAE	
Cyanolanius madagascarinus	*H. vangii*, *L. lairdi*, *T. avium*
Euryceros prevostii	*L. bennetti*, *L. lairdi*

Table 2. Continued.

Host species, by family	Parasite species identified
Falculea palliata	*H. vangii*, *P. parvulum*
Leptopterus viridis	*H. vangii*, *L. lairdi*
Newtonia amphichroa	*H. vangii*
Newtonia brunneicauda	*H. vangii*, *P. rouxi*
Schetba rufa	*L. bennetti*, *P. parvulum*, *T. avium*
Tylas eduardi	*L. lairdi*, *P. vaughni*, *T. avium*
Vanga curvirostris	*H. madagascariensis*, *H. vangii*, *L. bennetti*, *L. lairdi*, *P. parvulum*
ZOSTEROPIDAE	
Zosterops maderaspatana	*H. killangoi*, *H. zosteropis*, *L. zosteropis*

found to be parasitized. There was no statistically significant difference in prevalence of infection by endemic status ($P=0.52$).

Most of the birds sampled were classified by habitat preference as FDepS (434) or FDweS (475), and the remaining 38 birds were FEdgS. There was no statistical difference in infection prevalence between FDweS and FEdgS ($P=0.598$) or between FDepS and FEdgS ($P=0.083$); however, there was a significant difference between FDepS and FDweS ($P<0.0001$). Prevalence of parasite genera by habitat preference is detailed in Table 3. There was a significant difference in infection prevalence between dry forests (45.6%; 108/237) and humid forests (25.8%; 183/710) ($P<0.0001$). Detailed prevalence data by parasite genera is presented in Table 4.

Blood smears were made from birds collected at 11 different locations throughout Madagascar (Fig. 1). Prevalence by site (from north to south, forest type indicated) was as follows: Montagne d'Ambre (humid), 16% (7/45); Marojejy (humid), 32.4% (59/182); Anjanaharibe-Sud (humid), 21% (17/83); Namoroka (dry), 47% (15/32); Ambohitantely (humid), 20.0% (25/125); Andranomay (humid), 20.7% (25/121); Bemaraha (dry), 48% (31/64); Ankaratra (humid), 23% (3/13); Andringitra (humid), 33% (4/12); Morombe (dry), 44.0% (62/141); and Andohahela (humid), 33.3% (43/129).

Samples were obtained from elevations ranging from 60 m to 2,050 m above sea level, with no material available between 1,601 m and 1,800 m. Prevalence of hematozoan infection was highest at the lowest elevations, approaching half of the birds sampled. Detailed prevalence data overall and by parasite taxa by elevation are presented in Table 5. Microfilariae, as well as *Haemoproteus* and *Leucocytozoon* spp., were observed in each elevational range. *Babesia* spp. were observed in birds from a low-elevation humid forest site. Multiple infections were recorded in birds from across the elevational ranges.

DISCUSSION

Several large-scale studies have examined birds for hematozoa in the Neotropics (White et al., 1978), North America (Greiner et al., 1975), eastern and southeastern Asia (McClure et al., 1978), and central Europe (Kučera, 1981). The prevalence of parasitism observed in Madagascar (30.7%) is within the ranges reported in these studies. Bennett and Blancou's (1974) early hypothesis that hematozoan prevalence on Madagascar was low was almost certainly based on a small sample size. The current study, examining a larger sample of birds from a wider variety of sites and habitats, does not support that hypothesis.

In the Mascarene Islands, located to the east of Madagascar, prevalence avian hematozoa was 42%, emphasizing the success of ornithophilic vectors and susceptibility of birds in this region to

TABLE 3. Prevalence of parasitism by avian habitat preference (percentages unless otherwise indicated).

			Parasite[b]						
Habitat[a]	No. of birds sampled	Overall prevalence	P	H	L	Mf.	T	B	MI
FDepS	434	21.9 (95/434)	0.9	7.6	8.5	10.4	1.2		27.4
FDweS	475	38.5 (183/475)	2.7	26.7	10.5	10.3	0.4	0.4	27.3
FEdgS	38	34.2 (13/38)	2.6	13.2	5.3	15.8	2.6		5.3

[a] Habitat designations: FDepS = forest-dependant species; FDweS = forest-dwelling species; FEdgS = forest-edge species.

[b] P = *Plasmodium* spp.; H = *Haemoproteus* spp.; L = *Leucocytozoon* spp.; Mf. = Microfilariae; T = *Trypanosoma* spp.; B = *Babesia* spp.; MI = multiple infection.

infection (Peirce et al., 1977). Previous work on continental Africa demonstrated the considerable variation of parasite prevalence, ranging from 72% and 61.9% in Zaire and Uganda, respectively (Bennett and Herman, 1976; Valkiunas et al., 2005), to 39.8% in Zambia (prevalence of all sites combined; Peirce, 1984a), to 11.5% in Senegal (Bennett et al., 1978). Differences in prevalence between these sites are probably the result of variation in vector diversity and population size and avian community composition.

Like many other surveys of avian hematozoa (Greiner et al., 1975; White et al., 1978; Bennett et al., 1982; Peirce, 1984a; Murata, 2002), *Haemoproteus* spp. were the most frequently observed blood parasites in this current study, with 17.4% of the birds infected. Some possible explanations as to why this genus is so common might include regular reinfection such that parasitemias do not drop to undetectable chronic levels, or low morbidity and mortality associated with infection. However, unlike surveys done in nearby continental Africa (Bennett and Herman, 1976; Peirce, 1983, 1984a; Kirkpatrick and Smith, 1988; Sehgal et al., 2005), the next most prevalent hematozoan parasites were microfilariae. This suggests the presence of highly suitable vectors on Madagascar. Furthermore, it is possible that the species of filaroid nematodes in Madagascar have coevolved to exploit an available niche, particularly if further research determines they exhibit the same high degree of endemism as in the avian hosts.

Nearly 10% of the birds examined in this survey were infected with species of *Leucocytozoon*. This genus is typically frequently observed; in the nearby Mascarene Islands, the prevalence was as high as 47.8% on La Réunion (Peirce et al., 1977). Members of the Hippoboscidae are known to vector species of *Haemoproteus*, whereas *Leucocytozoon* spp. are transmitted by members of the Simuliidae. In addition, Ceratopogonidae are known to transmit both genera of parasites (Valkiunas, 2004). The higher prevalence of these parasite genera may reflect members of more than one family of vector

TABLE 4. Prevalence of parasitism by forest type (percentages unless otherwise indicated).

		Parasite						
Forest type	Overall prevalence	P	H	L	Mf	T	B	MI
Dry	45.6 (108/237)	3.4	29.9	3.8	21.5	0.4	—	26.9
Humid	25.8 (183/710)	1.4	13.1	11.3	6.8	1.0	0.3	26.2

[a] P = *Plasmodium* spp.; H = *Haemoproteus* spp.; L = *Leucocytozoon* spp.; Mf. = Microfilariae; T = *Trypanosoma* spp.; B = *Babesia* spp.; MI = multiple infection.

TABLE 5. Prevalence of parasitism by elevation ranges (percentages unless otherwise indicated).

		Parasite						
Elevation (m)	Overall prevalence	P	H	L	Mf	T	B	MI
60–400	46.8 (133/284)	3.9	30.6	5.6	20.8	0.7	0.7	28.6
401–800	29 (18/62)	1.6	17.7	11.3	3.2	—	—	16.7
801–1,200	29.4 (52/177)	2.3	10.2	13.6	12.4	1.1	—	26.9
1,201–1,600	19.1 (68/356)	0.6	10.1	8.4	4.2	0.8	—	22.1
>1,800	29.4 (20/68)	—	19.1	17.6	2.9	1.4	—	40

[a] P = *Plasmodium* spp.; H = *Haemoproteus* spp.; L = *Leucocytozoon* spp.; Mf. = Microfilariae; T = *Trypanosoma* spp.; B = *Babesia* spp.; MI = multiple infection.

contributing to parasite transmission in the area, although vector competence and vector capability may vary, and these vectors have not yet been identified.

The prevalence of *Plasmodium* spp. varies considerably from one study to another, and the 1.9% estimate reported here is similar to other large-scale surveys (Greiner et al., 1975; White et al., 1978; Bennett et al., 1982; Kirkpatrick and Smith, 1988; Murata, 2002). Research conducted in Uganda and Senegal both reported similar prevalences of avian *Plasmodium* spp. (1.2% and 1.7%, respectively), whereas a West African study reported a prevalence of 10.7% (Bennett et al., 1974, 1978; Sehgal et al., 2005). The high prevalence of *Leucocytozoon* spp. in Madagascar, compared with the related parasite genus *Plasmodium*, may reflect a more restricted host range for the hematophagous vectors culicine mosquitoes (Valkiunas, 2004). Whereas vector species of other Haemosporida may be more strictly ornithophilic, the vectors of avian *Plasmodium* spp. may feed on wider variety of vertebrate fauna, reducing their vector potential.

Species of *Trypanosoma* and *Babesia* were detected in less than 1.0% of birds sampled. The prevalence of *Trypanosoma* spp. is typically low, ranging from 0.2% in eastern and southeastern Asia to 7.3% in West Africa (McClure et al., 1978; Sehgal et al., 2005). To our knowledge, only two other studies, both performed in Uganda, reported *Trypanosoma* spp. as the second most common infection in birds (Bennett et al., 1974; Valkiunas et al., 2005). Finally, although *Babesia* spp. are rarely observed in birds, they are not unknown. Currently, there are 14 valid species of *Babesia* known from as many avian families (Peirce, 2005). Observations of these parasites during the current study were particularly surprising, because field researchers reported remarkably few ectoparasites such as ticks, the known vector of piroplasms, while examining captured birds.

Of the parasites that were identifiable to the species level, there were 25 species of *Haemoproteus*, 15 species of *Leucocytozoon*, five species of *Plasmodium*, and two species of *Trypanosoma* (Table 2). Among these 47 species, several are currently known only from Madagascar and presumed to be endemic. These taxa were previously unknown to science and were described as a result of this survey, and they include (percentage of species endemic to Madagascar in parentheses) five species of *Haemoproteus* (20.0%), five species of *Leucocytozoon* (33.3%), and one species of *Plasmodium* (20.0%). Of the parasite species identified during this study, 23.4% are known only from Malagasy birds (Table 1). By comparison, surveys on continental Africa reported fewer identified species. For example, 10 species of avian hematozoa were identified in Senegal; 28 species in Kenya, Tanzania, and Zaire; 29 species in Zambia; and eight species in the Mascarene Islands (Bennett and Herman, 1976; Peirce et al., 1977; Bennett et al., 1978; Peirce, 1984a). It is important to note that the level of bird species endemism, although not necessarily species richness, in these areas is considerably lower than on Madagascar. Hence, parasite species richness seems to mirror levels of isolation, as measured by degree of endemism of their avian hosts.

A few points should be mentioned about the newly identified species of Malagasy Haemosporida. Although *Plasmodium* spp. are not generally considered to have strong host specificity within avian taxa, *Haemoproteus* and *Leucocytozoon* spp. are host specific. Several classic investigations have provided empirical evidence of specificity of these two genera at the host family level (Fallis et al., 1954, 1974; Solis, 1973; Atkinson, 1986; Bennett and Peirce, 1988; Bennett et al., 1991). More recently, studies using mitochondrial DNA and cytochrome *b* sequences also have demonstrated a high degree of host family specificity in *Haemoproteus* spp. (Beadell et al., 2004; Fallon et al., 2005). As a result, taxonomic determinations in these genera are based on this host family specificity, and new parasites are named when previously uninvestigated host families are examined. Some argue that this is not a valid characteristic (Valkiunas and Ashford, 2002; Sehgal et al., 2006, Krizanauskiene et al., 2006; cf. Savage and Greiner, 2004).

Although the parasite species investigated in the studies mentioned above exhibit specificity at the host family level, some species of both *Haemoproteus* and *Leucocytozoon* are apparently host species specific (Baker, 1966; Greiner, 1991). At this time, we do not know how many of the currently named species exhibit this narrow degree of host specificity. Moreover, avian taxonomy is in flux as ornithologists further refine our understanding of avian phylogeny. This presents an additional challenge as we attempt to understand the relationship between hematozoan parasites and their hosts. Only experimental transmission studies of these parasites into different hosts can substantiate the validity of these taxa or demonstrate synonymy with other taxa. Thus, we continue to use the new species names from this survey until they are proven invalid.

In consideration of the host family specificity of *Haemoproteus* and *Leucocytozoon* spp., and the limited morphometric variation observed in avian *Plasmodium* spp., several new species of Haemosporida were described. Three new species, *H. forresteri*, *H. goodmani*, and *L. frascai*, were reported from the Brachypteraciidae (Savage and Greiner, 2004). Five new species, *P. parvulum*, *H. madagascariensis*, *H. vangii*, *L. lairdi*, and *L. vangis*, were described from the Vangidae (Savage et al., 2004, 2005, 2006b). *Haemoproteus khani* was reported from the Dicruridae (Savage and Greiner, 2005), and a previously described species, *H. dicruri*, also was observed (de Mello, 1935; Peirce, 1984b). Finally, one individual from the Sylviidae proved to be infected with a new species of *Leucocytozoon* distinct from those previously described, *L. atkinsoni* (Savage et al., 2006). Subsequent to the description of *L. atkinsoni* from *Neomixis tenella*, which was formerly placed in the Timaliidae, the taxonomy of numerous Malagasy passerines was re-evaluated and the type host belongs to the Sylviidae (Goodman and Hawkins, 2008). In addition, the morphology of this parasite was compared to the known species of *Leucocytozoon* from the Sylviidae and still considered valid. Finally, species of *Haemoproteus* and *Leucocytozoon* were observed in the Bernieridae, although species descriptions were not possible from these samples.

Prevalence of parasitism in the four endemic families or subfamilies sampled for this survey (Bernieridae, Brachypteraciidae, Philepittinae, and Vangidae), ranged from 14% in Bernieridae to 86% in the Brachypteraciidae. In addition, both the ground-rollers and the vangas had high numbers of multiple infections (67%

and 71%, respectively). These levels of parasitism may be a particular concern for conservation programs as more information regarding the pathogenicity of these parasites becomes available. The families with the highest prevalence of parasitism vary from one region to another. Because birds from the majority of Malagasy natural forest biomes were examined during these inventories, differences are not presumed to represent a sampling bias, but rather some behavioral, ecologic, or physiologic characteristic that increases the exposure of these birds to parasite vectors. The genus *Zosterops*, of the family Zosteropidae, had the highest prevalence of blood parasitism in Malagasy birds. This was also the case in Uganda and the Mascarene Islands (Bennett et al., 1974; Peirce et al., 1977). This family is represented on Madagascar by one endemic species, *Z. maderaspatana*, and can be found across a wide range of habitats from isolated gardens, small natural isolated forests, forest edge, and forest interior. It is also present on the western Indian Ocean Aldabra Atoll and Isle Europa, to the north and west of Madagascar, respectively. In 1971, 38 of 47 (80.9%) *Z. maderaspatana* sampled on Aldabra were infected with species of *Haemoproteus* (Lowery, 1971). Additional investigations are needed to examine the factors causing consistently high prevalence of infection in this family.

African Ploceidae commonly have high infection prevalence (Bennett et al., 1974, 1978; Peirce et al., 1977; Kirkpatrick and Smith, 1988). Four species of Ploceidae were represented in the current study. In addition to the high overall prevalence in this family, there was a notable difference associated with breeding systems. Prevalence of infection in the three solitary nesting species (*Foudia madagascariensis*, *Foudia omissa*, and *Ploceus nelicourvi*) was 43%, 25%, and 26% (Table 1), respectively, for a combined prevalence of 28%. In contrast, 75% of the colonial nesting *P. sakalava* had blood parasites. Higher prevalence of hematozoa in colonial breeders has been recognized previously (Kirkpatrick and Smith, 1988), and a recent literature review (Tella, 2002) further supports this point.

Other families surveyed in our study warrant additional mention, either for their high or low prevalence of infection. Of particular interest for its low prevalence (five of 90 individuals) is the Monarchidae, represented here by *T. mutata*. This species is abundant and commonly found in a variety of natural forest types and anthropogenic habitats across a broad range of elevations (Mulder and Ramiarison, 2003). When comparing *T. mutata* to another ubiquitous endemic Malagasy species with parallel habitat requirements, *Copsychus albospecularis*, the prevalence of hematozoan parasites was 22% in the latter (Table 1). Three remaining species are noteworthy for their high prevalence (regardless of sample size): *A. francesii* (Accipitridae), is a common regional endemic forest or woodland diurnal raptor, and 10 of 12 (83%) sampled were infected with blood parasites, all but one of which was *Leucocytozoon toddi*; *D. forficatus* (Dicruridae), a bird of forest and open habitat, and 14 of 18 (78%) were parasitized; and *O. rutilus* (Strigidae), generally of wooded habitat, and 13 of 18 (72%) were infected or coinfected with *Haemoproteus* spp., *L. danilewskyi*, or microfilariae (Tables 1 and 2). When habitat preference was considered, prevalence of infection was significantly higher in forest-dwelling species than in forest-dependant species. Although there was no statistical difference between forest-dwelling species and forest-edge species, far fewer forest-dwelling species birds were sampled. The difference in prevalence between different habitats is almost certainly related to the vector community present, as microhabitats vary widely between open areas, forest edges, and deep forest conditions. Although the majority of the birds were mist-netted in humid forest, birds from dry forest proved to have a significantly higher prevalence of blood parasites. Only infections with *Leucocytozoon* spp. were more prevalent in humid forest birds. Because many of the avian families sampled can be found in either habitat, it is likely that the higher prevalence of parasitism in birds collected in dry forests is related in some way to vectors. With limited water sources in the dry forests, it is possible that vector densities are greater and more concentrated. In addition, because there are fewer sources of water, more birds are forced to drink from a given source, and thus being exposed to vectors more frequently than may occur in humid forests where water sources are more plentiful. Finally, in three western low elevational sites, greater than 40% of the birds were infected with at least one type of blood parasite. Both overall prevalence and prevalence by host species has been reported to vary considerably in small geographic areas, usually in relation to vector abundance and species compositions (Sol et al., 2000; Shurulinkov and Chakarov, 2006). This is presumed to be the case at the Madagascar sites, with elevation, and local topographic and climatic factors influencing vector community compositions. The few surveys that report multiple infections indicate they are uncommon in avian hosts (Bennett et al., 1974; Murata, 2002). A much higher percentage of mixed infection was observed in the current study, apparent in more than one quarter of infected birds. Currently, we have no measures of the impact of multiple infections on host fitness. With at least 24% of parasites seemingly endemic, it is possible that they have evolved decreased pathogenicity, allowing infected birds to live longer, serve as reservoirs, and be fed upon by a greater variety of vectors.

At this time, the vectors of avian hematozoa in Madagascar are not identified. Dipteran taxa known to vector haemosporidian parasites in other regions are found in Madagascar. However, a tremendous number of endemic taxa are present, which also may participate in parasite transmission, for example, 80% amongst flies and up to 100% in culicines mosquitoes (Duchemin et al., 2003; Irwin et al., 2003). Of the 27 species of simuliids (black flies) currently known, 22 are endemic, and at least 13 more remain to be formally named (Elouard, 2003).

Identification of the vectors of avian hematozoa in Madagascar as well as investigations into pathogenic effects of avian hematozoa are necessary to gauge the true impact on Malagasy bird populations. This study provides a broad view of the status of avian hematozoa in Madagascar and should serve as a base for further research.

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