FULL PAPER *Parasitology*

Blood Parasites of Some West African Rainforest Birds

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ABSTRACT. A total of 969 birds representing 121 species of 21 families from the West African nations of Cameroon, Equatorial Guinea and Ivory Coast were examined for haematozoa using thin blood smears; 277 individuals (28.6%) harbored blood parasites. The parasites identified included species of *Haemoproteus* (7.7% prevalence), *Plasmodium* (10.7%), *Leucocytozoon* (4.6%), and *Trypanosoma* (7.3%). In addition, microfilariae of filariid nematodes were present in 3.6% of the individuals examined. The birds were collected over a period of 12 years, from 1989–2001, from rainforest and ecotone habitats. We report a relatively high prevalence of parasites in colonial nesting birds, and two species of ground nesting birds. In addition, we compared data from bird species collected at a site identical to a previously published study, and did not find significant differences in parasite prevalence between the two years constituting two different seasons. Our results are also compared to other studies in Africa that implement similar and different methodologies.

KEY WORDS: African rainforest bird, *Haemoproteus*, *Plasmodium*, *Trypanosoma*, *Leucocytozoon*.

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Blood parasites infect all vertebrates, and can affect the evolution and ecology of many species [8, 17]. Infection of birds is common, and it is estimated that 68% of all bird species are susceptible to haemosporidians [3]. These parasites can affect fitness and in some cases are pathogenic to their hosts [6, 26]. The most commonly studied avian blood parasites are the vector-borne parasites of the genera *Haemoproteus, Plasmodium, Trypanosoma* and *Leucocytozoon*. Microfilariae are also commonly found in avian peripheral blood [22]. Although the ornithological fauna of West Africa is highly diverse, the blood parasites of this avifauna have had only limited study [5,14,28]. Several recent studies have taken place elsewhere in Africa; for example a study of pigeons (*Columba livia*) in Uganda showed that 76.5% of the individuals tested were infected with species of *Haemoproteus* [10], and studies in South Africa have identified new species of *Haemoproteus* and other haematozoa [7]. Investigators have also suggested that birds of the semi-arid regions of South Africa lack haemotozoa due to the paucity of breeding habitats for insect vectors [15]. One study characterized the cestodes of 1,252 birds of 174 species from the Republic of the Ivory Coast, but in that study there was no mention of the blood parasites or nematode worms present in the individuals sampled [16]. Here we determine the prevalence of blood parasites in some bird populations of the African nations of Cameroon, Equatorial Guinea, and the Ivory Coast. These data establish a baseline of infection in these birds, and will be relevant to studies addressing how anthropogenic changes in habitat composition may influence parasite prevalence in the future.

MATERIALS AND METHODS

The samples used in this study were collected as part of an ongoing study of avian evolution in Central and West Africa [23, 24]. All birds were classified to Family based on the taxonomy of Sibley and Monroe [20]. Samples were collected over a period of 12 years (between 1989–2001) from Cameroon, Equatorial Guinea, and the Ivory Coast. The blood samples collected were obtained from a variety of habitats, including contiguous rainforest, fragmented rainforest sites in the ecotone (the transition zone between the rainforest and grassland [23]), and one montane site [24]. Rainforest sites are characterized by predictable periods of high rainfall, and consistent temperatures. The ecotone sites tend to have more variation in temperatures and rainfall. Collection sites in West Africa are shown in Fig. 1, and Table 1 lists the collection sites, the dates of sampling at each site, the habitat classification and the latitudinal and longitudinal coordinates of each site.

Birds were captured in mist nets and then released after taking a small amount of blood (~50 μl) via brachial venipuncture [21, 23]. Blood smears were made on site, and air-dried [14]. Following fixation in methanol, smears were stained with 3% Giemsa for 20 min, and examined using an Olympus BH compound microscope at 100×, 200×, 400×, and 1,000× for 20–50 min. Presence and intensity of parasites was recorded. Parasitemias were estimated using methods similar to those of Godfrey *et al.* [13]. Initially, lower magnifications (200× and 400×) were used, in order to detect microfilariae. Subsequently, 20 fields were observed at 1,000×, representing approximately 4,000 red blood cells. Each field observed at 1,000× contained approximately 200 red blood cells. Since parasitemias were most often very low, many more than 20 fields were typically examined, and intensity was still usually less than 1/4,000. Only parasitemias greater than 0.025% were quantified.

Representative smears have been deposited in the International Reference Centre for Avian Haematozoa, Queen-

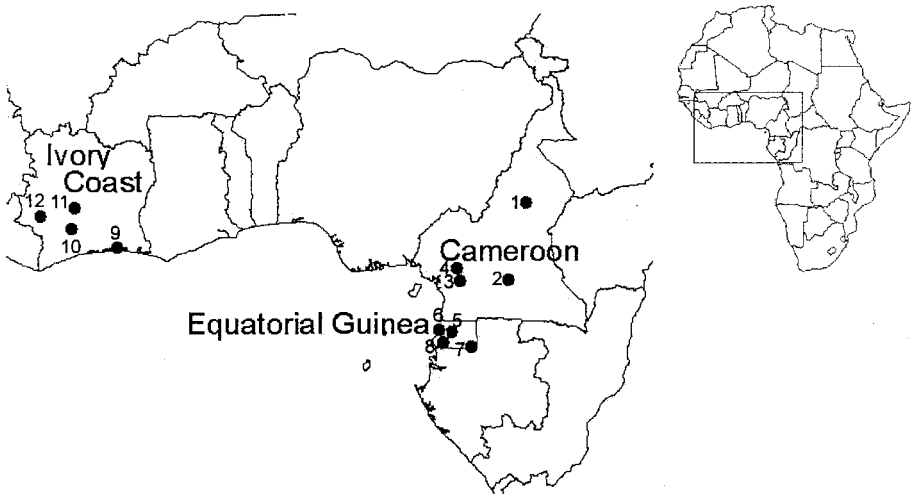

Fig. 1. Map illustrating the collection sites in Cameroon, Equatorial Guinea and the Ivory Coast. The numbers refer to the sites listed in Table 1.

Table 1. Dates and locations of collections

Site	Date	Location	Habitat type
Cameroon			
1. Ndibi	March-May 1989	N 3° 46.583' E 12° 12.616'	rainforest
2. Tibati	June 1995	N 6° 30.260' E 12° 35.280'	ecotone
3. Sakbayeme	May 2000	N 4° 02.290' E 10° 34.453'	rainforest
4. Sangmbengue	May 2000	N 4° 04.105' E 10° 33.683'	rainforest
Equatorial Guinea			
5. Mt. Alen	May 1998	N 1° 39.4' E 10° 18.9'	montane
6. Elende	May 1998	N 2° 12.98' E 9° 47.57'	rainforest
7. Mokula	May 1998	N 1° 02.86' E 11° 09.78'	rainforest
8. Ncoho	May 1998	N 1° 14.2' E 9° 57.11'	rainforest
Ivory Coast			
9. CSRS-Abidjan	Jan. 2000	N 5° 19.859' W 4° 07.743'	rainforest
10. Lamto	Jan. 2000	N 6° 12.957' W 5° 01.626'	ecotone
11. Marahoue	Jan. 2000	N 7° 01.680' W 5° 56.852'	ecotone
12. Tai Forest	June 2001	N 5° 49.981' W 7° 20.565'	rainforest

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RESULTS

A total of 969 birds, consisting of 121 species from 21 families and 8 orders were examined for blood parasites. Nearly all bird species sampled were either intra-African migrants or non-migratory. Table 2 lists the species sampled with the prevalence of blood parasites for each species. Of the birds examined, 28.6% were infected with blood parasites: 7.7% were infected with *Haemoproteus*, 10.7% with *Plasmodium*, 7.3% with *Trypanosoma*, 3.6% with microfilariae, and 4.6% with *Leucocytozoon*. Avian species with a relatively high prevalence of *Haemoproteus* included the brown-crested alethe (*Alethe poliocephala*) with 63% infected, and the red-headed quelea (*Quelea erythrops*) with 46% infected. *Plasmodium* species were found in 41% of the brown-crested alethe (*Alethe castanea*). *Trypanosoma* infected 21% of the green-tailed bristlebill (*Bleda eximia*) and *Leucocytozoon* infected 25% of *Q. erythrops* and 38% of Veillot's black weaver (*Ploceus nigerrimus*). The sister taxa, the white-tailed alethe (*Alethe diademata*) and *A. castanea* were commonly infected with microfilariae with 100% and 55% of the individuals infected respectively. The olive sunbird (*Nectarinia olivacea*) was highly prone to infections with 12% infected with *Haemoproteus*, 30% with Plasmodium, and 32% with *Trypanosoma*. Members of the Cisticolidae had low prevalence; only 1 of 37 (2.7%) individuals in this family had a blood parasite (*Plasmodium*). Infections with multiple genera were found in 53 of the 277 infected birds (19%) (Table 3). Table 3 also lists the number

Table 2. Prevalence of avian blood parasites classified by Family

Family	Species	# of Individuals Tested	# of Individuals Infected	Number infected with[a]					>1 parasite species/individual
				H	P	T	M	L	
Accipitridae	*Accipeter tachiro*	1	1	1					
Alcedinidae	*Alcedo cristata*	4	0						
	Alcedo leucogaster	5	1	1					
	Alcedo quadribracchys	1	0						
	Ceyx lecontei	4	1		1				
	Ceyx picta	11	2	1	1				
	Halcyon malimbica	10	3		3				
	Halcyon senegalensis	2	0						
Centropodidae	*Centropus senegalensis*	1	1	1[b]					
Cisticolidae	*Apalis sharpii*	1	0						
	Camaroptera brachyura	19	1		1				
	Camaroptera chloronata	1	0						
	Camaroptera superciliaris	2	0						
	Cisticola erythrops	5	0						
	Cisticola galactotes	2	0						
	Prinia bairdii	3	0						
	Prinia leucopogon	4	0						
Columbidae	*Turtur abyssinicus*	3	0						
	Turtur afer	20	3		2	1			
	Turtur brehmeri	2	0						
	Turtur tympanistria	11	2		2				
Corvidae	*Dicrurus ludwigii*	1	0						
	Laniarius erythrogaster	1	0						
	Platysteira castanea	9	1		1				
	Platysteira concreta	2	0						
	Terpsiphone ostridis	1	0						
	Terpsiphone rufiventer	13	2	2					
	Terpsiphone viridis	8	1	1					
	Trochocecrus nigromitratus	4	0						
	Trochocercus nitens	1	0						
Cuculidae	*Ceuthmochares aereus*	1	1		1				
	Chrysococcyx caprius	1	0						
	Chrysococcyx cupreus	1	0						
Eurylaimidae	*Smithornis rufolateralis*	1	0						
Hirundinidae	*Hirundo preussi*	2	0						
Indicatoridae	*Indicator exilis*	1	0						
	Indicator maculatus	1	0						
	Melignomon zenkeri	1	0						
Lybiidae	*Pogoniulus atroflavus*	1	1					1	
	Pogoniulus bilineatus	5	0						
	Pogoniulus scolopaceus	7	0						
	Pogoniulus subsulphureus	5	1					1	
	Trachyphonus purpuratus	1	1		1			1	X
Meropidae	*Merops varigatus*	5	0						
Muscicapidae	*Alethe castanea*	22	15		9	1	12		X
	Alethe diademata	4	4		1	1	4		X
	Alethe poliocephala	8	5	5		1			X
	Ficedula hypoleuca	1	0						
	Fraseria cinerascens	7	1	1[b]					
	Muscicapa comitata	1	1	1					
	Neocossyphus poensis	5	4	3		2	1		X
	Saxicola torquata	1	0						
	Sheppardia cyornithopsis	2	0						
	Stiphrornis erythrothorax	15	1			1			
	Stizorhina finschi	2	1	1					
	Stizorhina fraseri	5	2	1		1			
	Turdus pelios	1	1				1		
Nectarinidae	*Anthreptes collaris*	3	3		3				
	Nectarinia chloropygia	16	0						
	Nectarinia cuprea	2	0						
	Nectarinia olivacea	124	83	15[c]	37[e]	40	1	7	X
	Nectarinia reichenbachii	7	1			1			
	Nectarinia superba	2	1		1				

Table 2.-Continued

Family	Species	# of Individuals Tested	# of Individuals Infected	Number infected with[a] H	P	T	M	L	>1 parasite species/individual
Passeridae	*Amandava subflava*	1	0						
	Estrilda atricapilla	4	2	2					
	Estrilda melpoda	4	0						
	Euplectes afer	3	2	1	1				
	Euplectes ardens	1	0						
	Euplectes macrourus	7	1		1				
	Lonchura bicolor	3	2	2					
	Lonchura fringillidis	1	1	1					
	Malimbus nitens	6	0						
	Motacilla clara	1	1	1			1		X
	Nigrita bicolor	4	3	2	1[d]	2			X
	Nigrita canicapilla	2	2				2		
	Parmoptila woodhousei	4	1	1[b]					
	Ploceus aurantius	17	3	1				2	
	Ploceus nigerrimus	8	5	3	1			3	
	Ploceus nigricollis	4	0						
	Ploceus ocularis	1	0						
	Pyrenetes ostrinus	39	2	1	1				
	Quelea erythrops	24	15	11	1			6	
	Spermophaga haematina	13	3	3[b]					
Phasianidae	*Francolinus squamatus*	1	1		1				
Picathartidae	*Picathartes oreas*	1	1					1	
Picidae	*Campethera caroli*	5	2		1	1			
	Campethera nivosa	2	0						
	Verreauxia africana	4	0						
Pycnonotidae	*Andropadus gracillis*	2	0						
	Andropadus curvirostris	8	0						
	Andropadus latirostris	103	27	5[c]	8	4	3	13	X
	Andropadus virens	122	25	1	13	6		8	X
	Baeopogon indicator	1	0						
	Bleda canicapilla	32	4	1[b]	2	1			
	Bleda eximia	14	4			3	2		X
	Bleda syndactyla	4	2			1	2		X
	Chlorocichla flavicollis	14	0						
	Criniger calurus	1	1		1				
	Criniger chloronatus	4	2				2		
	Nicator chloris	9	1				1	1	X
	Phyllastrephus albigularis	8	1			1			
	Phyllastrephus icterinus	3	1		1				
	Phyllastrephus scandens	1	0						
	Phyllastrephus xaveri	2	2	2				1	X
	Pycnonotus barbatus	5	2		1	1	2		X
Rallidae	*Himantornis haematopus*	1	1	1					
	Limnocorax flavirostris	1	1	1					
Sylviidae	*Acrocephalus boeticatus*	1	0						
	Acrocephalus gracilirostris	1	0						
	Acrocephalus rufescens	2	0						
	Acrocephalus scirpaceus	2	0						
	Chloropeta natalensis	1	0						
	Hylia prasina	18	1			1			
	Illadopsis cleaveri	9	4	1	3				
	Illadopsis fulvescens	5	0						
	Illadopsis rufescens	4	0						
	Illadopsis rufipennis	6	3		1	1	1		
	Macrosphenus concolor	6	2		2				
	Macrosphenus flavicans	1	0						
	Sylvietta denti	1	0						
	Sylvietta virens	4	0						
Total	121 species	969	277	75	104	71	35	45	
	Percent of total infected		28.6	7.7	10.7	7.3	3.6	4.6	

a) Key: H= *Haemoproteus*, P=*Plasmodium*, T=*Trypanosoma*, M=microfilaria of filariid nematodes, L=*Leucocytozoon.* b) this may be P. c) two of these may be P. d) this may be H. e) three of these may be H.

Table 3. Prevalence of avian blood parasites at various collection sites

Site	Number infected with[a)] H	P	T	M	L	Number of multiply infected birds	Total infected birds	# of slides examined	Percent infected
CSRS-Abidjan	4	18	10	2	0	6	28	95	29.5
Elende	2	4	1	1	1	1	8	43	18.6
Lamto	3	10	4	0	0	0	17	92	18.5
Marahoue	0	5	7	0	0	1	11	64	17.2
Mokula	3	2	7	7	0	1	18	35	51.4
Mt. Alen	7	1	5	0	7	5	15	28	53.6
Ncoho	10	4	13	8	1	10	26	50	52.0
Ndibi	25	9	4	1	11	4	46	275	16.7
Sakbayeme	3	9	1	2	9	4	20	61	32.8
Sangmbengue	4	4	3	4	15	5	25	40	62.5
Tai Forest	11	32	14	8	1	14	52	111	46.8
Tibati	3	6	2	2	0	2	11	75	14.7
Totals	75	104	71	35	45	53	277	969	28.6

a) Key: H= *Haemoproteus*, P=*Plasmodium*, T=*Trypanosoma*, M=microfilaria of filariid nematodes, L=*Leucocytozoon*.

of infected birds found at each collection site. Note that in some cases, we were not able to distinguish whether the parasite was a species of *Haemoproteus* or *Plasmodium*, since the quality of the slides was sub-optimal; these samples are indicated in Table 2.

Most birds (98%) sampled showed low intensities of infection, with parasitemias less than 0.025%. However there were some striking examples of birds with high parasitemias. An individual African paradise-flycatcher (*Terpsiphone viridis*) collected at Tibati had a 20% parasitemia of *Haemoproteus*. Other birds with high parasitemias of *Haemoproteus* included an *A. poliocephala* captured at Mt. Alen (0.25%), two *A. poliocephala* caught at Ncoho (0.25% and 0.5%), one white-tailed ant-thrush (*Neocossyphus poensis*) from Ncoho (2%), and two *N. olivacea*, one caught at CSRS-Abidjan (0.3%), and one at the Tai forest. The single raptor caught in the study, an African goshawk (*Accipeter tachiro*) caught at Lamto, also had a very high parasitemia of *Haemoproteus*.

An African pygmy kingfisher (*Ceyx picta*) collected at Tibati had a very high parasitemia of *Plasmodium* as did one pale-breasted illadopsis (*Illadopsis rufipennis*) collected at the Tai forest, one *N. olivacea* collected at Lamto, and one *A. diademata* caught at Ncoho. One dwarf klngfisher (*Ceyx lecontei*) caught at Mokula harbored an unusual *Plasmodium* species that is most likely undescribed, and will be presented elsewhere. Similarly, one little greenbul (*Andropadus virens*) caught in the Tai Forest harbored an unusual trypanosome. Birds with high intensities of microfilariae included one yellow-whiskered greenbul (*Andropadus latirostris*) and one *A. diademata*, both caught at Mokula. One individual grey-headed negrofinch (*Nigrita canicapilla*) captured at CSRS-Abidjan had a high parasitemia of *Leucocytozoon*.

Many of the avian species studied here are documented for the first time with blood parasites. Since we have not yet identified parasites to the species level, we cannot recognize bird species as hosts for particular parasitic species. However, many of the avian species studied here have not been reported in the literature. For example, particularly interesting is the high prevalence of microfilariae in *A. diademata* and *A. castanea*. We have also seen no reports of *Haemosporida* in several of the kingfishers of the Alcedinidae family (*Alcedo leucogaster, C. lecontei, C. picta*, and *Halcyon malimbica*).

Table 4. Prevalences of blood parasites at one site in two different years

Species	Number infected/ Number examined Ndibi 1986[a)]	Ndibi 1989
Campethra caroli	0/3	1/4
Fraseria cinerascens	0/1	1/3
Anthreptes collaris	1/2	1/1
Nectarinia olivacea	6/9	3/8
Nectarinia reichenbachii	0/1	1/7
Estrilda atricapilla	2/5	1/2
Lonchura bicolor	3/7	2/3
Pyrenestes ostrinus	5/32	2/37
Spermophaga haematina	3/11	2/5
Euplectes afer	2/14	2/3
Euplectes macrourus	2/5	1/6
Ploceus aurantius	4/20	3/17
Ploceus nigerrimus	2/3	5/8
Quelea erythrops	4/11	15/24
Totals	34/124	40/128

a) From Kirkpatrick and Smith, 1988.

We did not find a significant difference in infection rates at one site in Cameroon, Ndibi, in the results from 1989 presented here as compared to our previously published study [14]. The data collected in 1986 took place in the rainy season from August-October ([14], www.worldclimate.com). In 1989, the birds were collected between March and May, before the onset of the heavy rains. Of the many species caught, fourteen bird species were sampled in both studies. Table 4 lists the species that were directly compared in the two studies. At Ndibi in 1986, 34 of 124 birds were infected with a blood parasite, and in 1989, 40 of 128 were infected (Table 4). Thus, when grouping together all avian species

and parasites, the prevalence of parasites did not differ significantly between the two years (Haber corrected binomial comparative trial χ^2_c=0.306, df=1, p≤1). Similarly, for any individual bird species, no significant differences between the two years were determined (data not shown).

DISCUSSION

The results of this study provide an indication of the prevalence of blood parasites in some West African rainforest birds. The overall prevalence of 28.6% of the individuals infected with blood parasites is relatively high compared to a study by Bennett *et al.* [5] in Senegal that reported an overall prevalence of 11.5%. Those birds were sampled in suburban Dakar, and the levels of infection were considered low in comparison to studies undertaken in other African nations [5]. The parasite prevalence of 28.2% reported for Uganda and 21.5% reported for Ghana are closer to what we report here [4, 5, 28], and the overall prevalence of 48.2% found in Balmoral, Zambia is higher [18]. Using microscopy, we found the prevalence of trypanosomes to be 7.3%. This is significantly lower than recent work we did studying similar birds using a polymerase chain reaction (PCR)-based assay with which we determined the prevalence of *Trypanosoma* to be 35% [21]. Similarly, a PCR-based assay found a prevalence of 40% for the avian-malaria causing parasites *Plasmodium* and *Haemoproteus* in blood samples collected from some of the same sites [19]. Combining the data for *Plasmodium* and *Haemoproteus* reported here with microscopy results in a prevalence of 18.5%, which is lower than the prevalence reported using the PCR assay. These findings point out that the two methods are discrepant, with the PCR-based assay reporting higher values, perhaps due to greater sensitivity [19, 21]. Optical microscopy of Giemsa-stained blood smears tends to be time-consuming and labor intensive, but is still considered the "gold-standard" for detection of parasites in blood. Recently, several methods, besides PCR-based assays, have been developed to detect parasites in blood; these include serological antigen detection, flow cytometry, and laser desorption mass spectrometry [9]. Parasitologists in the coming years will make use of the new and older technologies, and in making comparisons among studies it will be important to acknowledge differences in methodologies that may give discrepant results.

The birds were collected over a period of 12 years from 12 sites that share certain environmental components, but differ in others. Thus, in comparing the sites, it must be stressed that local insect vector populations can vary substantially with habitat type and season, and can thus influence the results of avian hematozoa surveys [1, 2]. We have very little knowledge of the insect vectors that transmit the parasites of these African rainforest birds. The vectors of *Haemoproteus* spp. in Africa may be midges (Ceratopogonidae) or louse flies (Hippoboscidae) [12]. The louse-fly *Pseudolynchia canariensis* has been implicated in the spread of *Haemoproteus* in *C. livia* of Uganda [10] but we have no knowledge that this is the same vector for the bird species studied here. Similarly, we have little knowledge of the vectors that transmit *Plasmodium*, and microfilarial nematodes. Black flies of the family Simuliidae typically cause the spread of *Leucocytozoon* [11]. In our study, the gallery forest sites where birds were collected very near to streams (Sangmbengue and Sakbayeme) which is typical breeding ground for black flies [5, 17] and where many black flies were observed (TB Smith, unpublished observations) yielded relatively high prevalences for that parasite (Table 3). Similarly, ornithophilic simuliid vectors tend to be abundant in montane regions, where streams are common [5], and at the one montane site where birds were collected, Mt. Alen, 25% of the individuals harbored *Leucocytozoon* (Table 3). At the other collection sites, *Leucocytozoon* was virtually absent, which is in concordance with the findings of Bennett *et al.* [5] with birds of Senegal.

The birds were collected from a range of habitats, over various seasons and from some sites that are distant from one another. No striking correlations could be inferred between parasite prevalence and site location, habitat or seasonal rainfall. In a direct comparison of data presented here with previously published data [14] from one site in Cameroon (Ndibi), we found no significant difference in the prevalence of avian haematozoa. These data suggest that the rainfall differences between the two years do not significantly influence the infection rates. In the first year, samples were taken during the heavy rain season, and in the second, samples were collected just prior to the heavy rainfalls. In another example, May is typically a period of high rainfall for the collection sites of Equatorial Guinea (www.worldclimate.com). However, the parasite prevalence at Elende, a coastal forest in Equatorial Guinea, in 1998 was 18.6%, and birds collected at Ncoho and Mokula (interior forest sites), also in Equatorial Guinea, in the same year had prevalences over 50%. These differences in parasite prevalence must be due to attributes other than rainfall, and are more likely due to the differences in habitat composition. Other factors contributing to differences in parasite prevalence could include proximity to breeding areas for vectors, relative levels of host resistance, local temperature differences, time of collection during the day, and age of the hosts, among other factors. It must also be noted that heavily infected individuals may be undersampled, as was shown in a study that found that birds with high parasitemias were underrepresented when caught in mist nets as compared to those sampled by gunshot [27].

Another factor influencing parasite prevalence is the behavioral ecology of the individual bird species. Colonial breeders are more susceptible to infection than congeneric non-colonial breeders according to a study by Tella [25], and also observed by Kirkpatrick and Smith [14], and Bennett *et al.* [5]. Again in this study (similar to the studies by Bennett *et al.* [5], and Kirkpatrick and Smith [14]), the ploceid colonial nesters, *P. nigerrimus* and *Q. erythrops* both had a blood parasite prevalence of 62.5% while the non-colonial nesting orange weaver (*Ploceus aurantius*) had a prevalence of 17.6%. These findings further assert that the

costs associated with parasitism may have influenced the evolution of colonial nesting [25]. Another interesting finding was the high prevalence of microfilariae in *A. castanea*, and the closely related *A. diadematа*. These birds are ground-nesters and have a distinctive odor (TB Smith, personal communication), but little is known about their behavioral ecology that may explain this finding. Interestingly, the congeneric species *A. poliocephala*, did not exhibit the same high prevalence of microfilariae. More information on the behavioral ecology of these birds will be required before we can infer why these species differ in their parasite loads.

We have established an important baseline of parasite prevalence for little-studied rainforest birds of Western Africa. With the high degree of deforestation and land use changes presently occurring in Africa, these data will be relevant to studies in the ecology of infectious disease, and especially how human-induced changes may affect host-parasite interactions.

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