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BLOOD PARASITES IN BIRDS FROM MONTEVERDE, COSTA RICA

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ABSTRACT: In a survey of avian blood parasites in Costa Rica, 51 (11%) of 479 birds sampled were infected by at least one species of hematozoan. Fourteen of the 60 species of birds in the survey were examined for the first time. Infections were most common in ramphastids and emberizids and infrequent in other taxa. Among resident species, infections were more commonly detected during the wet season when most birds breed than during the dry season when few birds breed. Infections caused by *Haemoproteus* sp. were most common, while *Plasmodium* sp., *Leucocytozoon* sp., *Trypanosoma* sp., and microfilarial infections were rare. The intensity of the 40 *Haemoproteus* infections in adult birds was low, with a mean \pm SE of 12.5 ± 3.7 infected cells per 10,000. *Haemoproteus* infections did not undergo seasonal changes in intensity.

Key words: Avian hematozoa, Neotropics, seasonality, *Haemoproteus*, *Plasmodium*, *Leucocytozoon*, microfilariae.

INTRODUCTION

Blood parasites (hematozoa) can cause extinctions and range contractions in birds (van Riper et al., 1986) and have been implicated in sexual selection and the evolution of bright plumage coloration (Hamilton and Zuk, 1982; Boyce, 1990; Pruett-Jones et al., 1990; Kirkpatrick et al., 1991). The importance of hematozoa to avian demography and evolution is potentially great, but our recognition of this importance is limited by our lack of knowledge concerning the distribution and prevalence of blood parasites, especially in tropical birds. Although several surveys have been conducted in the Neotropics (White et al., 1978; Bennett et al., 1980, 1991; Sousa and Herman, 1982; Woodward-Lynas et al., 1989; Garvin and Marra, 1991), no study has been published documenting the occurrence of avian hematozoa in the birds of Costa Rica. Furthermore, studies carried out in the tropics are generally of short duration and only Bennett et al. (1980) have addressed the seasonality of infections. Our objective was to determine the prevalence of hematozoa in birds sampled throughout the year at Mon-

teverde, Costa Rica, and compare the results with other studies in the Neotropics.

MATERIALS AND METHODS

Monteverde (10°18'N, 84°45'W) is located at 1,300 to 1,500 m elevation near the continental divide on the Cordillera de Tilarán. Strong northeast trade winds blow moisture in the form of mist during much of the December to April dry season. The winds subside during the intervening wet season. Most resident birds nest during the early wet season from May through July (Lawton and Guindon, 1981; Wheelwright, 1983; Winnett-Murray, 1986; B. Young and D. McDonald, unpubl.).

We trapped birds in Monteverde using mist nets about once each week from November 1990 through September 1991. To avoid resampling individuals, we marked birds by banding or cutting small notches in their rectrices and never netted in the same location more than once every 3 mo. We also included samples taken during a study of long-tailed manakins (*Chiroxiptia linearis*) at Monteverde (McDonald, 1989, 1993). The samples from the manakin project are from 1987 to 1991, and all of the species of birds in that study are also represented in the main 1990 to 1991 survey. The various mist net sites for both the main study and the manakin project were never closer than 250 m to each other. The habitat was 10 to 20-yr-old second growth and primary forest. The entire study area encompassed 2.6 km².

TABLE 1. Occurrence of blood parasites in adult and juvenile birds in Monteverde, Costa Rica, 1987 to 1991.

Taxon	Number of birds		Parasites present ^a				
	Examined	Infected	H	P	L	T	M
Ramphastidae							
<i>Aulacorhynchus prasinus</i>	7	3					3
Muscicapidae							
Turdinae							
<i>Catharus ustulatus</i> ^b	48	1	1				
<i>Hylocichla mustelina</i> ^b	1	1			1		1
<i>Turdus assimilis</i> ^c	1	1	1 ^d				
Vireonidae							
<i>Vireo philadelphicus</i> ^{b,c}	3	1			1 ^e		
Emberizidae							
Parulinae							
<i>Wilsonia pusilla</i> ^b	7	1	1			1	
Thraupinae							
<i>Chlorospingus ophthalmicus</i>	14	9	9				
Emberizinae							
<i>Atlapetes gutturalis</i>	16	11	11 ^d				
<i>A. brunneinucha</i>	8	6	6				1
<i>Melospiza leucotis</i> ^c	21	13	13 ^d	1 ^d			
<i>Tiaris olivacea</i>	10	1	1				
<i>Zonotrichia capensis</i>	9	3	3				
Uninfected species ^f	334	0					
Total	479	51	45	2	2	1	5

^a Number of birds with each parasite. H, *Haemoproteus* sp.; P, *Plasmodium* sp.; L, *Leucocytozoon* sp.; T, *Trypanosoma* sp.; M, microfilariiae.

^b North American migrant.

^c First time species examined for blood parasites.

^d New host record.

^e North American migrant examined for the first time on the wintering grounds.

^f Uninfected species (number of individuals examined): Columbidae: *Geotrygon chiriquensis* (1), *Leptotila verreauxi* (1); Momotidae: *Momotus momota* (5); Capitonidae: *Semnorris frantzii* (1); Picidae: *Melanerpes hoffmani* (1); Furnariidae: *Premnoplex brunnescens* (3), *Thripadectes rufobrunneus* (1); Dendrocolaptidae: *Dendrocincla homochroa* (19), *Sittasomus griseicapillus* (7), *Xiphorhynchus erythropygius* (2), *Lepidocolaptes souleyetii* (1); Formicariidae: *Dysthymus mentalis* (3), *Myrmotherula schisticolor* (1); Tyrannidae: *Zimmerius villosus* (9), *Elaenia frantzii* (5), *Mionectes olivaceus* (35), *M. oleagineus* (5), *Rhynchocyclus brevirostris* (2), *Platyrinchus mystaceus* (5), *Empidonax flavescens* (5), *Myiarchus tuberculifer* (2), *Megarhynchus pitangua* (1), *Myiodynastes hemichrysus* (1); Pipridae: *Chotrixiphia linearis* (90); Corvidae: *Cyanocorax morio* (1); Troglodytidae: *Thryothorus rufalbus* (8), *T. modestus* (5), *Troglodytes aedon* (20), *T. ochraceus* (1), *Heterorhina leucosticta* (1), *H. leucophrys* (13); Muscicapidae, Turdinae: *Myadestes melanops* (16), *Catharus aurantirostris* (7), *C. fuscater* (4); Emberizidae, Parulinae: *Vermivora peregrina* (1), *Dendroica pensylvanica* (1), *D. virens*^{b,c} (1), *Oporornis formosus* (1), *Geothlypis poliocephala* (1), *Wilsonia canadensis* (3), *Myioborus miniatus* (23), *Basileuterus culicivorus* (10), *B. rufifrons* (3), *B. tristriatus* (1); Coerebinae: *Coereba flaveola* (1); Thraupinae: *Tangara icterocephala* (1), *Euphonia hirundinacea* (4); Icterinae: *Molothrus aeneus* (1).

We made blood smears from a drop of blood taken from the brachial vein. After air drying, we fixed slides from 100% methanol the same day they were collected and later applied Giemsa stain (Bennett, 1970). We examined smears first under low power magnification (400×) for trypanosomes and microfilariiae and then under oil immersion (1,000×) for smaller hematozoa. We examined approximately 100,000 cells per

smear, so the chance of not detecting an infection was minimal (Godfrey et al., 1987). For *Haemoproteus* infections, we scored the intensity of the infection as the number of cells infected per 10,000 cells examined. We then deposited all samples in the collection of the International Reference Centre for Avian Haematozoa (IRCAH), Memorial University of Newfoundland, St. John's, Newfoundland, Can-

ada (accession numbers 120536–120587). The IRCAH personnel confirmed our identifications of the parasites.

To examine seasonality, we compared parasite prevalence during the December to April dry season to prevalence during the May to November wet season. Because we were interested only in patterns for resident birds, we excluded migrant species. Furthermore, we restricted the analysis to species in which we found at least one infected individual (defined here as susceptible species). To avoid the confounding effects of the influx of juveniles during the wet season, we analyzed samples from adults only. Sample sizes were inadequate to perform separate comparisons for each species, so we combined all species to make one single comparison. Thus we assumed that if parasites cycled seasonally, they did so similarly in all host species.

We compared the overall prevalence of hematozoa in our study to that of other Neotropical studies. While this general comparison blurs distinctions between parasite taxa, it is a useful assessment of the relative importance of blood parasites in a community of hosts. Surveys of Neotropical faunas vary in the number of North American migrants represented, and North American migrants are much more likely than resident species to harbor *Leucocytozoon* infections which they acquire on the breeding grounds (White et al., 1978). To remove this bias, we calculated the prevalence of hematozoa in resident bird species only from this study and recalculated parasite prevalences for resident birds in surveys from the literature.

Throughout, our nomenclature of birds follows that of the American Ornithologists' Union (1983). We performed all statistical tests using SYSTAT (Wilkinson, 1989).

RESULTS

We found blood parasites in 11% of the birds we examined (Table 1). Of the 60 species evaluated, 14 had not previously been examined for blood parasites, based on White et al. (1978) and Sousa and Herman (1982), including two North American migrant species (Table 1). Infections were most commonly found in ramphastids and emberizids; other taxa were remarkably free of infection (Table 1).

Haemoproteus was by far the most common hematozoan. *Haemoproteus coatneyi* was most common but found only in emberizines; all infected brush-finches (*Atlapetes* sp.), white-eared ground-spar-

rows (*Melospiza leucotis*), and chestnut-collared sparrows (*Zonotrichia capensis*) harbored *H. coatneyi*. *Haemoproteus thraupi* was restricted to common bush-tanagers (*Chlorospingus ophthalmicus*), whereas *H. fallisi* was only found in a Swainson's thrush (*Catharus ustulatus*). *Leucocytozoon* occurred only in North American migrants. The one wood thrush (*Hylocichla mustelina*) in the sample was infected by *L. shaartusicum*. We found *Plasmodium relictum* in a ground-sparrow and a yellow-faced grassquit (*Tiaris olivacea*). Microfilariae occurred in emerald toucanets (*Aulacorhynchus prasinus*), the wood thrush, and a chestnut-capped brush-finch (*Atlapetes brunneinucha*). The single *Trypanosoma* sp. infection was in a migrant Wilson's warbler (*Wilsonia pusilla*).

Seventeen (46%) of 37 samples collected during the December through April dry season from adults of susceptible species were infected with at least one species of hematozoa. Twenty-eight (71%) of 34 wet season samples from adults of susceptible species showed infections; based on a chi-square test, this seasonal difference was significant ($P = 0.04$). Samples of adults with *Haemoproteus* infections had a mean (\pm SE) of 12.5 ± 3.7 infected cells per 10,000 (range, 1 to 120). However, with a Mann-Whitney test there was no significant difference in counts of cells infected with *Haemoproteus* per 10,000 cells examined for samples collected in the dry (mean \pm SE, 17.6 ± 7.3 ; $n = 17$) versus the wet season (8.7 ± 3.4 , $n = 23$) ($P = 0.26$). The analysis was weakened, however, because 19 of the 40 samples with *Haemoproteus* infections had only one infected cell per 10,000. Thus low intensity infections were common.

The prevalence of blood parasites in resident Monteverde birds was 12%.

DISCUSSION

The low prevalence of blood parasites (12%) reported here is typical for the Neotropics and was well within the range re-

ported for resident birds in other Neotropical regions (Puerto Rico: 3% (Garvin and Marra, 1991); El Salvador: 4% (Winchell, 1978); Bolivia: 5% (Bennett et al., 1991); Colombia: 7% (Bennett and Borrero, 1976); Jamaica: 8% (Bennett et al., 1980); Panama: 18% (Sousa and Herman, 1982)). It was substantially lower than in Nearctic avifauna in which hematozoa prevalence averaged 37% (Greiner et al., 1975). Others have pointed out that this might result from a low availability of insect vectors in the tropics (Bennett and Borrero, 1976; White et al., 1978; Sousa and Herman, 1982; Bennett et al., 1991; Garvin and Marra, 1991). For example, the species of ornithophilic black flies that serve as vectors for *Leucocytozoon* spp. may be rare in the tropics. We found *Leucocytozoon* only in North American migrants as previously reported by Bennett et al. (1980); these birds probably were infected on the breeding grounds where ornithophilic simuliids can be abundant. *Culicoides* spp. (Diptera: Ceratopogonidae) and hippoboscids flies, the primary vectors known for *Haemoproteus*, also may be less common in the tropics than in the temperate zone. If vector abundance limits dispersal by blood parasites, we might ask why have tropical blood parasites not evolved to exploit vectors that are common in the tropics? With the great diversity of blood sucking Diptera in the Neotropics, it seems that there has been ample opportunity to exploit a new vector. Perhaps phylogenetic constraints have prevented parasites from adapting to definitive hosts other than the particular dipteran taxa with which they evolved (Barta, 1989).

Although blood parasites are less common in Neotropical than other systems, we cannot yet assume that they are any less important. If a parasite is aggregated in a few individuals in a population of birds, it may seem unimportant. Even a seemingly rare parasite could nevertheless regulate the host population if it has intermediate virulence (Anderson and May, 1978; Toft, 1991). Although none of the

infected birds we handled appeared unhealthy, studies in which the virulence of avian hematozoa in the tropics is examined are needed before we can be sure about the importance of hematozoa to populations of tropical birds.

There was a wide range in prevalence of parasites within families of birds (Table 1). Bennett et al. (1980) noted that families with North American centers of origin had higher prevalences of hematozoa than families with South American centers of origin. The same was true for this study. Northern groups such as turdines, vireonids, thraupines, and emberizines had higher parasite prevalences than southern groups such as dendrocolaptids, piprids, and troglodytids. Yet there were exceptions, such as the primarily South American Ramphastidae (43% prevalence). Recently Ricklefs (1992) found that parasite prevalence at the level of family was negatively correlated with incubation period. Species with relatively long incubation periods (with respect to their egg size) generally had lower prevalences than species with short incubation times. Ricklefs (1992) suggested that long incubation times presumably allowed birds to better develop their immune systems and therefore to be more resistant to infection. Both ramphastids and thraupines have relatively short incubation times (Ricklefs, 1992), which may explain why they seem to be especially susceptible to parasites. This correlation between incubation time and resistance is suggestive, and detailed field studies of the ecology and epizootiology of specific host-parasite systems are needed to confirm this relationship.

We found mixed evidence that blood parasites are seasonally distributed at Monteverde. Birds sampled during the wet season had higher parasite prevalences than birds sampled during the dry season. Yet the intensity of *Haemoproteus* infections did not vary with season. These results should be interpreted with caution, however, because the wet and dry season samples were not evenly distributed among

taxonomic groups. Another problem is that we collected most of the data during only one year, although we note that rainfall during the year of the study (2,641 mm) was close to the 31 year average for Monteverde (2,538 mm).

Nonetheless, the period of higher parasite prevalence, the wet season, corresponded with the breeding seasons of most host species sampled. Based on North American models (Beaudoin et al., 1971), the breeding season is exactly when we should see a relapse of hematozoa. Similarly, Bennett et al. (1980) found the lowest prevalence of hematozoa in Jamaican birds during November and December when birds there do not breed. Based on our preliminary results, we propose that tropical hematozoa can have seasonal rhythms that resemble those of temperate hematozoa.

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