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ISLAND AND TAXON EFFECTS IN PARASITISM AND RESISTANCE OF LESSER ANTILLEAN BIRDS

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Abstract. Patterns of parasitism in insular avian communities can provide insight into processes that maintain host–parasite associations. On one hand, replicable relationships within evolutionarily independent communities of the same host and parasite taxa would indicate that these interactions are stable over time. On the other hand, unique ecological conditions on each island, sporadic colonizations and extinctions, plus new genetic variation would lead to island-specific host–parasite relationships. We examined the distribution of three parasitic taxa among avian host species on three islands in the Lesser Antilles: St. Lucia, Martinique, and Dominica. Blood protozoa of the genus *Haemoproteus* were found in 34% of host individuals examined. A significant species effect, but no significant island effect, was observed, suggesting an ecologically stable and replicable host–parasite association. Cysts of the tissue-dwelling protozoan genus *Sarcocystis* were observed in 4% (9% on Dominica) of host individuals and were significantly associated with ground foraging. Epithelial lesions characteristic of avian papilloma virus were recorded in 4% of host individuals on Martinique only. The pattern of infection with papilloma virus or *Sarcocystis* (significant island effect) indicated that host species on a particular island are linked in transmission webs of these parasites. Such island-specific associations suggest a role for either history or unique local ecology in host–parasite associations.

There was a statistically significant interaction between island and species effects in the prevalence of *Haemoproteus*. This may stem from the independent evolution of host–parasite interactions in the different island populations. We were able to assess the extent of genetic divergence of the host species by analysis of mitochondrial ATPase 6,8 sequences. There was little genetic divergence between island populations of the host species. Therefore, the variation in *Haemoproteus* prevalence is not likely to be related to genetic differentiation of the host populations.

Birds infected with *Haemoproteus* exhibited elevated leukocyte levels indicative of immunological control of the parasite. After statistically controlling for the intensity of *Haemoproteus* infection and host species, leukocyte levels varied significantly among islands on which the host resided. This is consistent with the idea that insular avian communities are linked by transmission webs of parasites having broad host specificity.

Key words: blood parasites; Haemoproteus; *hematozoans; host–parasite interactions; immune response; Lesser Antilles; leukocyte counts; papilloma virus;* Sarcocystis.

INTRODUCTION

The dynamics and organization of communities of parasites having many vertebrate hosts has proven to be a challenging problem for ecologists and evolutionary biologists. Theoretical models have considered the population dynamics of such interactions (May and Anderson 1979, Hudson et al. 1985, Crawley 1992), including the role of the immune response (Norman et al. 1994). Although empirical investigations have lagged, in part because of the complexity of natural communities (e.g., Aho and Bush 1993), temporal and spatial variation in parasite prevalence and infection by pathogens suggest complex, spatially heterogeneous dynamics in host–parasite systems on ecological scales, evolutionary scales, or both (van Riper et al. 1986, Prins and Weyerhaeuser 1987, Atkinson et al. 1988, Atkinson and Van Riper 1991, Yezerinac and Weatherhead 1995).

Empirical studies of temporal and spatial heterogeneity in parasite–host interactions are most informative when comparisons are made among discrete populations. Longitudinal studies of geographically circumscribed host populations can provide insight into the ecological and evolutionary dynamics of multiple host–parasite relationships (Forbes et al. 1994, Bennett et

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al. 1995, Merilä et al. 1995), but inferences may be obscured by temporal or spatial variation in the data.

The roles of ecological and evolutionary factors in the outcome of host–parasite interactions can be teased apart statistically by examining a set of species over several discrete localities, such as isolated islands. In this case, island effects represent unique attributes of individual islands, which may include the array of habitats on each island, composition of the host community, and presence of suitable vectors and reservoirs for parasites. To the extent that an island effect may result from community composition, it may also, in part, reflect stochasticity of colonization and extinction independent of an island's ecology. Host-specific effects may arise because of unique genetic or ecological attributes of each type of host. From the standpoint of host–parasite evolution, the most revealing source of variation is the host × island interaction, which indicates the extent of unique outcomes of host–parasite relationship in a particular host across a set of ecologically defined locations. Such statistical interactions could result from island-specific genetic factors in the host resulting from founder events and mutation. Host–parasite coevolution, i.e., reciprocal genetic changes in host and parasite populations, would also have to be considered as a possibility.

Several studies have addressed the distribution of parasites across island populations, but these have lacked suitable sampling to detect host × island interactions. An analysis of the gut helminth parasites of *Anolis* lizards in the Lesser Antilles related variation in parasitism to the distribution of hosts among habitats within islands rather than to ecological differences between islands associated with area or altitude (Dobson and Pacala 1992). Repeatable associations between parasites and hosts thus appear to follow upon environmental factors. However, disjunct distributions of many parasites suggested that historical factors, such as colonization and extinction, may have influenced the particular assemblage of parasite species within each host population (Dobson and Pacala 1992). Because *Anolis* comprises only one or two morphologically distinct species on most islands, it is difficult to resolve whether the observed patterns represent the evolutionary outcome of host–parasite interactions or purely stochastic processes.

Surveys of island avifaunas in the Indian Ocean likewise indicate considerable heterogeneity in the distribution of blood parasites. *Haemoproteus* spp. and *Plasmodium* spp. infect passerine birds on Aldabra (Lowery 1974), but haemoproteids are rare on the Mascarene Islands (Pierce et al. 1977) and absent in the Malagasy Republic (Bennett and Blancou 1974). *Leucocytozoon* spp. infections have not been observed in Aldabra, but are frequent in the Mascarene Islands and Malagasy Republic. Presence or absence of a blood parasite from a particular area may depend on the presence or absence of competent insect vectors. Strong island effects and turnover of the avifaunas between islands preclude the estimation of island × host interactions in these data.

In this study, we present data on haematozoan parasite prevalence and white blood cell counts for six species of passerine bird on three adjacent islands in the Lesser Antilles. The host species were the Bananaquit (*Coereba flaveola*), Antillean Elaenia (*Elaenia martinica*), Lesser Antillean Bullfinch (*Loxigilla noctis*), Streaked Saltator (*Saltator albicollis*), Black-faced Grassquit (*Tiaris bicolor*), and the Black-whiskered Vireo (*Vireo altiloquus*). Data were collected during a single, brief period in 1991. Our sampling design allowed us to estimate island and host effects as well as host × island interactions. Significant host effects in the prevalence of the protozoan parasite *Haemoproteus* spp. demonstrated that the sampling program was large enough to discern statistically significant host–parasite combinations. Moreover, blood leukocyte counts, which indicate an individual host's response to its parasite load (Fallis et al. 1951, Desser et al. 1968), show that both deterministic and historical factors shape host–parasite associations. Finally, we suggest a framework for gauging the relative importance of these factors based on island biogeographic analysis.

Study Area and Methods

This study was conducted on St. Lucia, Martinique, and Dominica, Lesser Antilles, between 20 July and 10 August 1991. These islands are similar in size (616–1100 km^2) and reach elevations (960–1450 m) that create a variety of habitats ranging from montane forest to dry lowland scrub (Beard 1949, Lack 1976). We sampled both wet and dry habitats in different parts of each island to obtain a representative sample of each island's avifauna. To some extent, the sample sizes (9–37 individuals per island population) reflect the relative abundances of the host species on each island. Birds were captured with mist nets at the following locations (and dates): on St. Lucia, Edmond Forest Preserve (20–22 July), and Anse La Sorciere (23–25 July); on Dominica, Springfield Plantation-Mt. Joy Estate (27–29 July), Syndicate Estate (30–31 July), Ponte Casse (1 August), and Glanvillia Quarry (2 August); on Martinique, Arboretum (6–7 August), Point Rouge (8 August), Le Francoise (9 August), and Grand Fond (10 August).

Blood samples were taken by jugular venipuncture and smears were prepared and fixed in absolute methanol in the field. Blood smears were stained in Giemsa in order to visually identify leukocytes and parasites. Hemoparasite and leukocyte levels were estimated in five randomly chosen fields at 400× magnification (Russo et al. 1986) and are expressed as the number of parasites or leukocytes per 13 000 erythrocytes. Hemoparasite and leukocyte identifications follow Campbell (1988) and Hawkey and Dennett (1989). All microscopy was performed by the same observer (N. Yorinks). Prevalence refers to the percentage of hosts in-

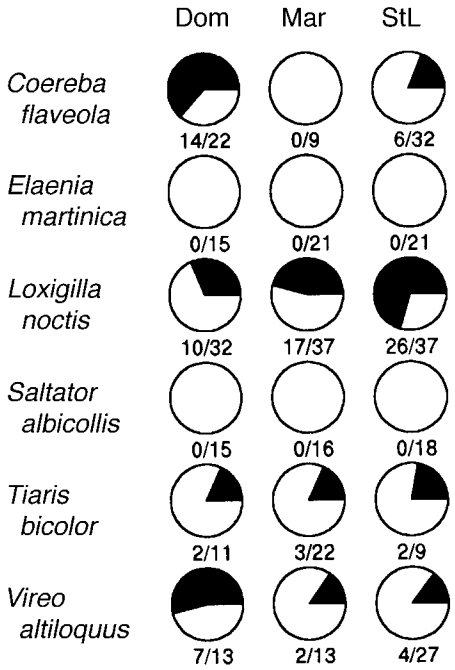

FIG. 1. Prevalences of *Haemoproteus* sp. in samples of six avian host species on the islands of Dominica (Dom), Martinique (Mar), and St. Lucia (StL), Lesser Antilles. The solid portion of each pie diagram represents infected individuals. Figures below each pie diagram are numbers of individuals infected/total samples.

fected and parasitemic intensity, or parasitemia, refers to the number of parasites per 13 000 erythrocytes.

All birds underwent physical examination of the superficial surfaces, especially featherless areas (Harrison and Ritchie 1994), to detect the distinctive skin lesions attributable to papilloma virus infection (Gerlach 1986) and the characteristic intramuscular ''rice-grain'' macrocysts of the protozoan parasite *Sarcocystis* spp. (Box et al. 1984).

Pectoral muscle biopsies and blood samples were collected nondestructively from all captured birds (Seutin et al. 1993) and were preserved as described in Seutin et al. (1991). All samples were collected and transported under the appropriate permits and licenses. DNA extractions in the laboratory of E. Bermingham followed the protocol of Seutin et al. (1993). We amplified a 1074 bp segment of mtDNA that spanned the full tRNALys, ATPase 8, and ATPase 6 genes by polymerase chain reaction (PCR) with the primer pair CO2GQL and CO3HMH. (Primer sequences and amplification conditions are available upon request from E. Bermingham.) Amplification products were cleaned electrophoretically and purified by adsorption onto silica in the presence of high salt buffer (Geneclean procedure, Bio101, Vista, California, USA), and were sequenced in the L direction using DyeDeoxy Terminator Cycle Sequencing (Applied Biosystems Division of Perkin Elmer, Foster, California, USA) with the primers CO2GQL, LYSL, PKL, PKLD, and TPL. Nucleotide sequences were determined by electrophoresing purified amplified product in an Applied Biosystems 373A DNA sequencer.

Estimates of interpopulation nucleotide divergence were based on the overlapping coding region (841 base pairs) of the ATPase 6 and ATPase 8 genes. Pairwise divergences of silent nucleotide substitutions between individual sequences were calculated according to Takahata and Nei (1985) and Takahata (1989).

We used SAS/STAT version 6.08 (SAS Institute 1990) to estimate correlation coefficients within island populations (PROC NESTED) and to perform ANOVAs (PROC GENMOD) of parasitemic intensity and leukocyte levels. Host species and island effects in contingency tables of parasitic infection were estimated using PROC CATMOD. The contingency table analysis accounts for the nature of the prevalence data (frequencies) and the unbalanced sample sizes. These will be explained in more detail, along with other statistical tests.

RESULTS

Blood protozoa

Gametocytes of *Haemoproteus* spp. (the only blood parasite observed) appeared in blood smears of four of the six avian host species scored on each island (Fig. 1). The pooled prevalence rate was 34%. Five of the six species were consistently infected or uninfected across the three islands included in this study. A categorical model relating *Haemoproteus* infection to host species and island revealed a significant species effect, but no island effect, and a significant host × island interaction (Table 1).

Of the four species infected with haemoproteids, the probability of infection varied significantly among islands in *Coereba flaveola* (log-likelihood $\chi^2 = 13.0$, df = 2, $P = 0.0015$), *Loxigilla noctis* ($\chi^2 = 10.2$, df = 2, $P = 0.006$), and possibly *Vireo altiloquus* ($\chi^2 = 7.1$, df = 2, $P = 0.03$). Prevalence of *Haemoproteus* in *Tiaris bicolor* did not vary among islands ($\chi^2 = 0.4$, df = 2, $P = 0.84$).

For *Loxigilla noctis*, the prevalence of haemoproteid infection did not differ significantly between sites on the same island (habitat effect: $\chi^2 = 0.6$, df = 1, $P = 0.45$), although prevalence did differ significantly between islands (island effect: $\chi^2 = 11.4$, df = 2, $P = 0.003$; Table 2). On St. Lucia, sufficient numbers of three species were captured to assess differences be-

TABLE 1. Categorical model of the prevalence of *Haemoproteus* infections with respect to host species and island.

Source	df	χ^2	P
Intercept	1	60.7	<0.0001
Species	5	40.4	<0.0001
Island	2	2.3	0.311
Species × island	10	28.1	0.0017

TABLE 2. Prevalence of hemoproteid infections in selected island populations with respect to habitat.

		Habitat					
		Dry			Wet		
Host species	Island	Infected	*n*	Percentage infected	Infected	*n*	Percentage infected
Coereba flaveola	St. Lucia	5	20	25	1	12	8
Vireo altiloquus	St. Lucia	2	9	22	2	16	13
Loxigilla noctis	St. Lucia	16	22	73	10	15	67
Loxigilla noctis	Martinique	2	11	18	13	23	57
Loxigilla noctis	Dominica	3	10	30	6	21	29

Notes: The table reports the number of individuals infected by *Haemoproteus*; *n* indicates the total sample.

tween sampling sites. The analysis revealed that prevalence did not differ significantly between sites ($\chi^2 = 1.2$, df = 1, $P = 0.26$), despite significant differences among host species ($\chi^2 = 22.0$, df = 2, $P < 0.0001$; Table 2).

There were no discernible differences of intensity of haemoproteid infection among infected individuals of the four species known to be infected (Poisson regression, PROC GENMOD: log-likelihood $\chi^2 = 3.2$, df = 3, $P > 0.15$). For *Loxigilla noctis* (shown in Fig. 2), the sample size was sufficient to test whether intensity differed between islands, but significant differences could not be detected (log-likelihood $\chi^2 = 1.5$, df = 2, $P > 0.15$).

Genetic distances between island populations

Populations of the six species included in this study are relatively undifferentiated over the islands of St. Lucia, Martinique, and Dominica (Table 3), although a strong genetic disjunction has been observed in the Bananaquit *Coereba flaveola* between the islands of St. Lucia and St. Vincent (Seutin et al. 1994). Average pairwise genetic distances between haplotypes on different islands (percentage of nucleotide substitution) varied from a low of 0.06% for *Saltator albicollis* between Martinique and St. Lucia to a high of 0.49% for *Loxigilla noctis* between the same two islands. Average pairwise nucleotide divergence within islands for several populations for which we obtained sequences for three or more individuals was similar to between-population distances: *Coereba flaveola* (Dominica, 0.08%, $n = 3$; St. Lucia, 0.10%, $n = 9$); *Loxigilla noctis* (Martinique, 0.56%, $n = 3$; St. Lucia, 0.23%, $n = 5$). Thus, these island populations of these species appear to be differentiated weakly, if at all.

Tissue parasites

Cysts of *Sarcocystis* sp. were observed in skeletal muscle of 8 of 27 potential host species sampled on Dominica, 2 of 20 species on Martinique, and none of 21 species on St. Lucia (Table 4). A categorical model of the presence or absence of *Sarcocystis* in hosts on the three islands revealed a weak island effect ($\chi^2 = 5.4$, df = 2, $P = 0.067$). Of seven host species with eight or more individuals sampled on each island, *Sarcocystis* was found in three (*Saltator albicollis*,*Tiaris bicolor*, *Loxigilla noctis*) on one island (Dominica), whereas only one infected individual of *Loxigilla noctis*

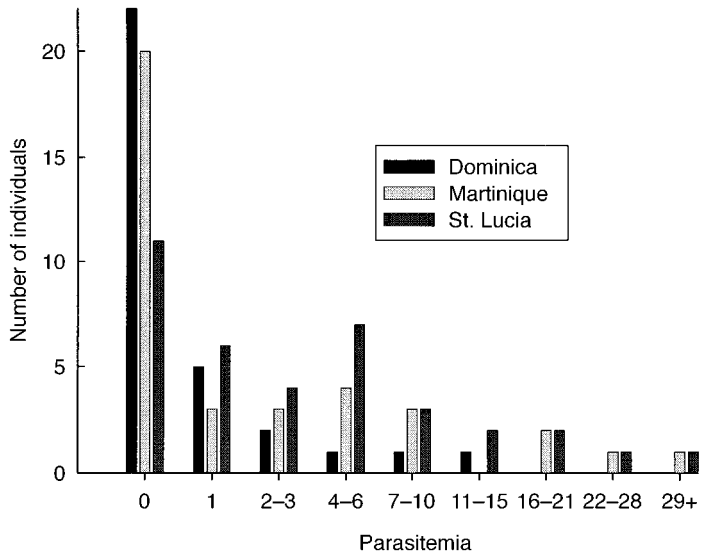

FIG. 2. Distributions of parasitemias in island populations of *Loxigilla noctis.* Units of parasitemia are numbers of *Haemoproteus*-infected cells per 13 000 erythrocytes.

TABLE 3. Average pairwise genetic distances between ATPase 6,8 mtDNA sequences from individuals of five host species on different islands.

Host species	Sample size			Distance (%)		
	DOM	MAR	STL	D–M	D–S	M–S
Coereba flaveola	3	2	9	0.16	0.07	0.17
Elaenia martinica	1	1	2	0.24	0.24	0.00
Loxigilla noctis	2	3	5	0.36	0.43	0.49
Saltator albicollis	2	2	2	0.35	0.42	0.06
Tiaris bicolor	2	2	2	0.24	0.43	0.18

Notes: D, DOM is Dominica; M, MAR is Martinique; S, STL is St. Lucia.

was found on another island (Martinique). Because of the small sample of species, this distribution is not significantly heterogeneous ($\chi^2 = 2.6$, df = 2, $P = 0.27$). An additional five species were infected with *Sarcocystis* on Dominica, whereas only one other species (*Myiarchus oberi*) was found to be infected on another island (Martinique).

Skin lesions indicative of papilloma virus infection were found in only seven island populations, six of these on the island of Martinique (Table 4). In spite of the small sample size and an overall prevalence of only 1.5%, this pattern was heterogenous enough to produce a significant island effect ($\chi^2 = 7.2$, df = 2, $P = 0.027$).

Leukocyte levels

We counted four types of leukocytes: heterophils (or neutrophils), eosinophils, monocytes, and lymphocytes. Lymphocytes are undifferentiated agranulocytes, which are apparently involved in production of antibody. Monocytes also lack granules and are primarily phagocytotic, as are the granulated heterophils. The function of the granulated eosinophils is less well understood, but may be related to extracellular defense against large parasites, such as helminths (Roitt et al. 1989). Of the four types of leucocytes, the abundances of only heterophils and eosinophils were significantly correlated within island populations ($r = 0.21$, $n = 352$, $P < 0.01$; Table 5), indicating relative independence in the levels of these cell types in the blood. All

TABLE 4. Prevalence of *Sarcocystis* sp. infection (Sar.) and papillomatous lesions (Pap.) in Lesser Antillean birds.

Host species	Dominica					Martinique					St. Lucia				
	Sar.		Pap.			Sar.		Pap.			Sar.		Pap.		
	Inf.	%	Inf.	%	*n*	Inf.	%	Inf.	%	*n*	Inf.	%	Inf.	%	*n*
Coereba flaveola	0	0	0	0	24	0	0	0	0	12	0	0	0	0	32
Eulampis jugularis	0	0	0	0	20	0	0	0	0	12	0	0	0	0	29
Elaenia martinica	0	0	0	0	15	0	0	1	4	25	0	0	0	0	22
Vireo altiloquus	0	0	0	0	13	0	0	1	8	13	0	0	0	0	27
Myadestes genibarbis	0	0	0	0	4	0	0	0	0	24	0	0	0	0	3
Margarops fuscus	0	0	0	0	4	0	0	0	0	1	0	0	0	0	6
Contopus latirostris	0	0	0	0	1	0	0	0	0	1	0	0	0	0	5
Geotrygon montana	0	0	0	0	3	0	0	0	0	1	0	0	0	0	3
Saltator albicollis	1	7	0	0	15	0	0	1	6	16	0	0	0	0	18
Tiaris bicolor	2	18	0	0	11	0	0	1	4	24	0	0	0	0	8
Loxigilla noctis	10	19	0	0	52	1	3	0	0	40	0	0	0	0	37
Dendroica petechia	1	14	0	0	7	0	0	1	10	10					
Dendroica plumbea	6	21	0	0	28										
Margarops fuscatus	1	50	0	0	2										
Troglodytes aedon	1	11	3	33	9										
Turdus plumbeus	4	57	0	0	7										
Sericotes holosericeus	0	0	0	0	16										
Buteo platypterus	0	0	0	0	1										
Cichlherminia lherminieri	0	0	0	0	1										
Chaetura martinica	0	0	0	0	1										
Myiarchus oberi	0	0	0	0	5	1	20	3	60	5					
Cyanophaia bicolor	0	0	0	0	9	0	0	0	0	5					
Columbina passerina	0	0	0	0	3	0	0	0	0	9					
Tyrannus domincensis	0	0	0	0	3	0	0	0	0	1					
Zenaida aurita	0	0	0	0	20	0	0	0	0	2					
Cinclocerthia ruficauda	0	0	0	0	8						0	0	0	0	2
Orthorhynchus cristatus	0	0	0	0	5						0	0	0	0	3
Quiscalus lugubris						0	0	0	0	4	0	0	0	0	3
Mimus gilvus						0	0	0	0	3	0	0	0	0	3
Turdus nudigenis						0	0	0	0	1	0	0	0	0	7
Dendroica adelaida											0	0	0	0	10
Buturides virescens											0	0	0	0	1
Icterus laudabilis											0	0	0	0	4
Ramphocinclus brachyurus											0	0	0	0	5
Melanospiza richardsoni											0	0	0	0	3

Notes: Inf. indicates the number of individuals infected by either *Sarcocystis* (Sac.) or papilloma virus (Pap.); *n* is the total sample; and % is the percentage of individuals infected.

TABLE 5. Pearson product-moment correlation coefficients (r) within island populations; species and island effects were first removed by nested ANOVA. Correlations for all individuals are presented above the diagonal; only individuals parasitized by *Haemoproteus* are included in values below the diagonal.

	Haemo	HET	EOS	MON	LYM	WBC
Haemo		**0.172**	0.031	0.070	0.059	**0.169**
HET	**0.295**		**0.205**	0.021	0.011	**0.704**
EOS	0.118	0.093		0.132	0.043	**0.489**
MON	0.128	−0.132	0.248		0.097	**0.637**
LYM	0.135	−0.069	−0.142	0.059		**0.280**
WBC	**0.368**	**0.755**	**0.338**	**0.486**	0.217	
Mean	1.50	4.38	0.93	4.45	0.89	10.65
1 SD	4.72	7.27	3.04	6.44	2.23	11.13

Notes: *Haemo* is the intensity of *Haemoproteus* infection; HET is heterophils; EOS is eosinophils; MON is monocytes; LYM is lymphocytes; and WBC is total leukocytes (i.e., HET + EOS + MON + LYM). Significant correlations ($P < 0.01$) are indicated in boldface.

four types of leukocytes summed give the leukocyte, or white blood cell (WBC), count. This summary variable was normally distributed following log transformation. Here, we present results only for WBC counts because additional analyses of individual leukocyte types (not shown) did not provide additional or conflicting information.

Among individuals infected with *Haemoproteus*, leukocyte levels were positively correlated with parasitemic level ($r = 0.39$, $P < 0.01$, $n = 82$; Table 5), due primarily to a correlation between heterophil level and parasitemia ($r = 0.30$, $P < 0.01$, $n = 82$). WBC levels were elevated in individual birds infected with haemoproteids, compared to noninfected individuals, after species and island effects were removed (Table 6). WBC levels were also significantly correlated with the intensity of infection (parasitemia), over and above the heterogeneity of parasitemia with respect to individual species and islands (Table 7). WBC levels were not related to *Sarcocystis* and papilloma virus infection, nor to the interaction of these tissue parasites with haemoproteid infection (analyses not shown).

WBC levels differed significantly between avian host species and islands (Tables 6 and 7, Fig. 3). The interaction between these two effects was of marginal statistical significance ($P = 0.06$), and became nonsignificant ($P > 0.15$) when haemoproteid intensity was included in the model. Thus, it appears that a significant component of the variance in WBC levels can be attributed to blood parasite (*Haemoproteus*) infection, but that additional significant components can be attributed to both island and host species. This is consistent with the significant host effects observed in haemoproteid infections and significant island effects observed in *Sarcosystis* spp. and papilloma virus infections; these effects might apply to other parasite organisms not monitored in this study.

TABLE 6. ANOVA of log-transformed leukocyte levels with respect to host species, island, and presence or absence of infection by *Haemoproteus*. Only the four species known to be infected are included.

Source	df	Type III sum of squares	MS	F	P	r^2
Species	3	10.8	3.6	6.1	0.0005	0.18
Island	2	13.9	7.0	11.8	<0.0001	
Infection	1	4.8	4.8	8.2	0.0044	
Error	257	151.3	0.6			

Notes: Least squares means: infected, 2.57; uninfected, 2.26 ($\log_e$ units/13 000 cells). Interactions were found to be nonsignificant and were deleted from the model.

DISCUSSION

This analysis has revealed strong species effects and species × island interactions in *Haemoproteus* infections, and significant relationships of leukocyte counts to *Haemoproteus* infection and parasitemia. Furthermore, there were significant species and island effects over and above the response of leucocytes to *Haemoproteus*. These results suggest species-specific variation in the interactions of hosts with their pathogens, as well as independence of individual island populations with respect to their interactions with pathogens.

Differences in hematozoan prevalence among Lesser Antillean, Jamaican, and mainland (Panama) populations

The comparability of our sample from the Lesser Antilles with those of other studies depends, in part, on the temporal stability and seasonal consistency of hematozoan prevalences. In a sample of almost 1600 resident birds on the island of Jamaica, Bennett et al. (1980) found that prevalence varied seasonally, from a low during the fall and winter to a high during the spring and summer, which encompasses the period of our study. In addition, many individuals were recaptured over periods of three months or more. Of individuals infected at the time of their initial capture, about half (9/20) lost traces of the infection on blood smears; a much lower percentage of apparently unin-

TABLE 7. ANOVA of log-transformed leukocyte levels of birds infected with *Haemoproteus* with respect to host species, island, and intensity of infection (number of *Haemoproteus* gametocytes per 13 000 erythrocytes).

Source	df	Type III sum of squares	MS	F	P	r^2
Species	3	4.5	1.5	9.9	<0.0001	0.38
Island	2	5.4	2.7	7.2	0.001	
Infection	1	3.0	3.0	7.2	0.009	
Error	86	31.3	0.4			

Notes: Only the four species known to be infected are included. Interactions were found to be nonsignificant and were deleted from the model.

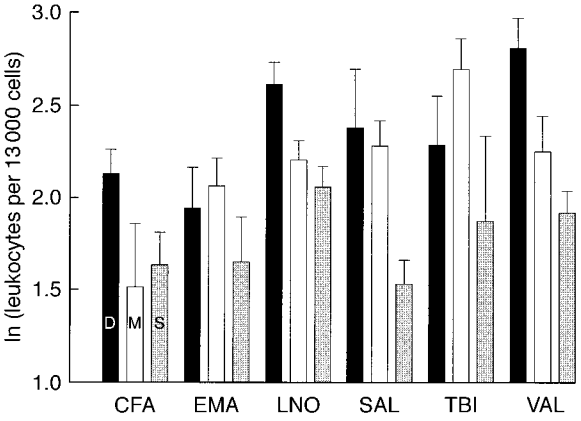

FIG. 3. Mean (+1 SE) leukocyte levels (natural logarithm of the number of leukocytes per 13 000 erythrocytes) in the blood of six avian host species on the islands of Dominica (D, black), Martinique (M, white), and St. Lucia (S, gray). Both species and island effects were significant (see Tables 6 and 7). Host species abbreviations are: CFA, *Coereba flaveola*; EMA, *Elaenia martinica*; LNO, *Loxigilla noctis*; SAL, *Saltator albicollis*; TBI, *Tiaris bicolor*; and VAL, *Vireo altiloquus.*

fected birds (9/283 = 3.2%) either gained infections or their parasitemias increased above the threshold of detection. Because individuals seem to lose infections at a high frequency, and because the percentage of infected individuals exhibited significant seasonal variation, it is important that different locations be compared at the same season of the year. Our study was conducted at a time (toward the end of the breeding season) when prevalences of blood parasites should have been high.

We did not attempt to identify parasites to the species level. In the case of *Haemoproteus,* new species are described when parasites exhibit distinctive morphology in a new host species (Bennett et al. 1994). At present, it is uncertain whether morphological variation reflects genetic differences between parasites on different hosts, or host-induced phenotypic differentiation in a single population of parasites (Atkinson 1991, Bury-Caines and Bennett 1992). Resolution of this issue awaits genetic analyses of *Haemoproteus* on different hosts.

Haemoproteid infections are common in neotropical passerines found within the Caribbean region. *Coereba flaveola* showed low prevalence (<5%) of *Haemoproteus* on Jamaica (Bennett et al. 1980) and in Panama (Galindo and Sousa 1966, Sousa and Herman 1982). This is consistent with our observations from Martinique (0 of 9 infected), but contrasts with the higher prevalence in this species found on Dominica (14/22 = 64%). The low prevalence of infection on Jamaica further emphasizes the between-island heterogeneity that we observed in this species.

The absence of visible haemoproteid infection in *Elaenia martinica* in this study is consistent with the low prevalence of *Haemoproteus* in other species of *Elaenia* in continental localities (3–10%; White et al. 1978, Sousa and Herman 1982) and on Jamaica (10%; Bennett et al. 1980). In view of the heterogeneity observed within some species, including the genetically undifferentiated *Coereba flaveola* on Dominica and Martinique (Seutin et al. 1994), one would not necessarily expect such consistency among different species within a genus, even though hematozoan prevalence does exhibit family-level heterogeneity (Ricklefs 1992).

The genus *Loxigilla* is endemic to the West Indies; hence, comparison of hematozoan prevalence in *L. noctis* can only be made with other species in the same subfamily (Emberizidae: Emberizinae). Haemoproteid infection in emberizines on Jamaica was quite low (3%; Bennett et al. 1980) and averaged 10% in Panamanian (Sousa and Herman 1982) and South American populations (White et al. 1978). Within the Emberizinae, infection varies greatly, although prevalences >30% are unusual for neotropical finches (White et al. 1978). Thus, the high prevalence of *Haemoproteus* spp. infection in *L. noctis* and the variation between islands is noteworthy. Among other emberizines, the prevalence of *Haemoproteus* in *Tiaris* (7/42 = 17%) would appear to be typical; the absence of *Haemoproteus* (0/49) from *Saltator* (Emberizinae: Cardinalinae) lies in striking contrast.

The prevalence of haemoproteid infection in *Vireo altiloquus* is not unusual compared to other neotropical species of the genus *Vireo*. On Jamaica, for example, 44% of *Vireo altiloquus* were similarly infected (Bennett et al. 1980). For vireonids in general, prevalence was 23% for Panama (Sousa and Herman 1982) and 14% for the neotropics (White et al. 1978); prevalences of all hematozoans together in tropical Vireonidae were 34% (White et al. 1978).

Other blood parasites

There was no evidence of *Leucocytozoon* spp. infection in the Lesser Antillean avifauna. This parasite was also absent from a survey of nonmigratory Jamaican birds, yet small numbers of wintering temperate migrants were found to harbor *Leucocytozoon* spp. (Bennett et al. 1980). On Cuba, a survey of 45 birds comprising 20 species failed to detect *Leucocytozoon* infections (Zajicek and Mauri Mendez 1969). Furthermore, *Leucocytozoon* is infrequent in the blood of tropical birds in general (White et al. 1978). It is not known whether this is related to the distribution and abundance of their principal vectors, simulid flies, in the tropics.

Infections with *Plasmodium* spp. were not observed in the Lesser Antilles, although plasmodial infections have been reported for *Coereba flaveola* from Jamaica (6/139 = 4%; Bennett et al. 1980) and Panama (1/24 = 4%; Sousa and Herman 1982). *Plasmodium* infections have also been reported in *Tiaris bicolor* from Jamaica (1/46 = 2%; Bennett et al. 1980) and in *Sal-*

tator albicollis from Panama (1/54 = 2%; Sousa and Herman 1982). Emberizids typically have a low prevalence of malaria: 5% in the continental neotropics (White et al. 1978) and 2% on Jamaica (Bennett et al. 1980). *Plasmodium* infection was observed on Cuba, but as a rare (<1%) infection of domestic chickens (Zajicek and Mauri Mendez 1969). We also did not observe trypanosomes or microfilariae in peripheral blood smears. Blood smears can detect infection by these hematozoa, but are thought to have low diagnostic sensitivity (Bennett 1962). Despite this fact, trypansome infections were found in *Coereba flaveola* (1/24 = 4%), *Tiaris bicolor* (2/46 = 4%), and *Vireo altiloquus* (1/55 = 2%) from Jamaica (Bennett et al. 1980). In Panama, trypanosome infections have been recorded for *Coereba flaveola* (1/24 = 4%; Sousa and Herman 1982). Microfilarial infections have been reported for *Coereba flaveola* from Jamaica (1/139 = 1%; Bennett et al. 1980) and for *Coereba flaveola* (1/24 = 4%) and *Saltator albicollis* (1/54 = 2%) from Panama (Sousa and Herman 1982). It is possible that *Plasmodium, Trypanosoma,* and microfilaria infections were overlooked in our populations, but it is doubtful that these species would have provided additional biogeographic information.

Effect of host species

The prevalence of *Haemoproteus* varied significantly among host species; it was absent from *Elaenia martinica* and *Saltator albicollis.* The strong species effect suggests either that each species is infected by a genetically differentiated population of the parasite, or that exposure to vectors of the parasites or resistance to the disease itself varies among hosts. *Haemoproteus* is transmitted by sandflies, or biting midges, of the genus *Culicoides* (Diptera: Ceratopogonidae; Harwood and James 1979, Kettle 1982), and by louse-flies (Diptera: Hippoboscidae; Kettle 1982), both of which occur in the Lesser Antilles (Bequaert 1954, Wirth 1974). The two species lacking haemoproteids in our sample were captured in the same areas and forest strata (understory) as species that were heavily infected. There were also no obvious differences in feeding ecology of infected and noninfected species. Thus, the distribution of haemoproteids among host species suggests that variation in prevalence is due to unique attributes of each host–parasite interaction.

The observation that particular bird species are consistently infected with *Haemoproteus* across islands implies that suitable vectors are not limiting. This leads to the prediction that hippoboscid louse flies are the most important vectors, because these ectoparasites would be transported by their hosts during colonization events. In addition, hippobocids are more likely to be restricted to particular host species than are free-living ceratopogonid midges. Unfortunately, little is known of the host specificity of the hippoboscid and ceratopogonid vectors of *Haemoproteus* or of the parasites themselves.

Sarcocystis is known to have a wide avian host range, but transmission between host species evidently requires contact with the ground (Box et al. 1984). The distribution of *Sarcocystis* among potential hosts is consistent with transmission through soil. On Dominica, the only island with substantial occurrence, *Sarcocystis* was found in 6 of 11 entirely or partly ground-feeding species of bird, but in only 2 of 16 species that rarely or never forage on the ground ($\chi^2 = 5.5$, df = 1, $P < 0.025$).

Papilloma virus spreads by direct transmission through the air (Gerlach 1986), so one might assume that infection would be more prevalent among abundant species than among less common ones. Except for *Troglodytes aedon* on Dominica, papilloma virus infections were almost completely restricted to Martinique. Of the six species represented by more than 12 individuals in our sample, four carried papilloma infections, whereas only two of 14 species with 12 or fewer individuals were infected. However, prevalences were low (generally <10%), so our ability to detect infections in small samples was limited. Infected species exhibited no obvious ecological attributes in common. Together with the strong island effect evident for papilloma virus, virtually restricted to Martinique, this suggests between-island differences in the overall community ecology of the total host–parasite complex. Presumably, this effect must be linked to aspects of the transmission of the disease, including the possibility of introduction from poultry, pet birds, or contaminated material transported to the islands.

Island effects

Prevalence of *Haemoproteus* sp. did not vary significantly among islands (Table 1). *Sarcocystis* was found almost exclusively on Dominica, and papilloma virus infections on Martinique. Birds on St. Lucia were apparently free of both diseases. Considering the distribution of these diseases over bird species, regardless of their abundance in our sample, these distributions were significantly heterogeneous in the case of papilloma virus ($P = 0.027$) and marginally so in the case of *Sarcocystis* ($P = 0.067$). The island effect for *Sarcocystis* may reflect the presence on Dominica of a suitable mammalian reservoir for the disease (Box et al. 1984), but this idea has not been assessed directly. There is no such ready explanation for the distribution of papilloma virus, but its localization may reflect unique genotypes of the pathogen on Martinique, coupled with broad infectivity across potential hosts.

Species × island interactions

Although no island effect was evident in the prevalence of *Haemoproteus,* several species exhibited significant, but independent, variation in prevalence among islands (the species × island effect in Table 1).

In the absence of information on host specificity of *Haemoproteus,* the simplest explanation for these statistical interactions invokes genetic variation in resistance to *Haemoproteus,* or in host-specific patterns of infectivity by a shared pathogen, or both. Based on mtDNA haplotypes, none of the six species in this sample exhibits significant genetic divergence between islands. Other species do show significant divergence indicative of independent evolution of populations over the same set of Lesser Antillean islands (E. Bermingham and R.E. Ricklefs, *unpublished observations*). It is possible that there is no longer effective gene flow between island populations of the species in this sample, but that there has not been enough time for these populations to accumulate unique mtDNA variation. Genetic factors related to disease resistance, such as genes of the major histocompatibility complex, may diverge under strong selection much more rapidly than mtDNA. It is also possible that generalized pathogens may have evolved different spectra of infectivities as a result of their relationships with other hosts on a particular island.

Mitochondrial DNA sequences are generally thought to diverge at a rate of 2% per 10^6 years, representing a nucleotide substitution rate of 10^{-8}/yr (Shields and Wilson 1987, Bermingham and Lessios 1993, Knowlton et al. 1993, Tarr and Fleischer 1993; see Klicka and Zink 1997: note 11). Genetic distances between haplotypes in different island populations range between ~0.1% and 0.5% in our sample, which may not significantly exceed distances between haplotypes within island populations. Even if between-island distances represent significant genetic divergence (the three populations of *Loxigilla noctis,* e.g., have no haplotypes in common in our small sample), estimated time since evolutionary isolation would be a maximum of 50 000–250 000 years, and almost certainly much less. Therefore, any genetic effects that may have produced differences in *Haemoproteus* prevalence among island populations of the same species must have arisen over periods of tens of thousands of years (generations), which is consistent with selective enhancement of available genetic variation, but less so with the production of new genetic variation by mutation.

Immune system activity

The significant difference between species in WBC levels is consistent with the strong species effect in prevalence of *Haemoproteus* (Bennett and Hawkey 1988, Hawkey and Bennett 1988). The positive relationship between WBC levels and the intensity of haemoproteid infection recalls hematological changes that accompany infection with other avian hematozoa, such as *Leucocytozoon* spp. (Fallis et al. 1951, 1956, Desser et al. 1968). Even after factoring out the presence/absence or intensity of *Haemoproteus* infection, species effects on levels of blood leukocytes remained significant (Tables 6 and 7). This suggests either that other parasites not monitored in this study also vary significantly among species, or that the general response of leukocyte counts to infection varies in a species-specific manner.

It was surprising, however, that within the entire sample of host species, island effects on white blood cell counts were significant even after statistically controlling for host species and blood parasite intensity. Apparently, unrelated hosts that are members of the same community are uniformly responding to yet-unidentified parasites that may have broad host specificity but restricted distribution over islands. Leukocyte data thus indicate that unrelated species inhabiting the same community (island) are linked, possibly through parasites of broad host specificity. These agents might be arthropod-transmitted viruses, water contaminated with enteric bacteria, or helminths whose infective eggs and larvae are found in soil and invertebrate hosts.

Immunological characterization of community-wide host–parasite interactions

In addition to providing information on the distribution and prevalence of particular parasites in specific hosts in great detail, comparison of immunological parameters among hosts and location may provide a simple, indirect characterization of the organization of local host–parasite associations and their consistency between localities. Analysis of variance in leukocyte levels can identify effects of species, location, and season, as well as quantify the intrinsic variation in response to parasitism within a local population at a particular time.

Surveys of blood parasites in bird populations suggest a high degree of geographic heterogeneity in the prevalence of any particular infectious agent (Forbes et al. 1994, Bennett et al. 1995, Merilä et al. 1995, Yezerinac and Weatherhead 1995). This variation makes it difficult to assess the overall level of infection in a population as a whole from studies of individual parasites. Our hematological results show that leukocyte levels are sensitive to a prominent blood parasite, but also appear to respond to other infectious agents not surveyed. Thus, leukocyte levels are likely to provide a general index to the prevalence of infections within a population.

It is commonly believed that bird populations in a natural community are linked by pools of circulating parasites, but as yet this has been poorly documented. The island effect on leukocyte abundance strongly implies the existence of local infectious agents widely shared among different hosts. Such patterns could be explored further by examining host immunologic responses and immunogenetic variation. Circulating levels of cytokines and immunoglobulins can provide corroborative information on the generalized activity of the immune system. The distribution of major histocompatibility complex genes in the host populations would provide relevant immunogenetic information

(Apanius et al. 1997). These indicators would not only integrate information from a variety of parasitic exposures, but also provide a better mechanistic understanding of these ecological interactions.

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