Articles

J. Avian Biol. 000: 000–000, 000
doi: 10.1111/j.1600-048X.2011.05404.x

Subject Editor: Jan-Åke Nilsson. Accepted 31 July 2011

Distribution anomalies in avian haemosporidian parasites in the southern Lesser Antilles

Robert E. Ricklefs, Julia Dodge Gray, Steven C. Latta and Maria Svensson-Coelho

R. E. Ricklefs (ricklefs@umsl.edu), J. D. Gray and M. Svensson-Coelho, Dept of Biology, Univ. of Missouri – St Louis, One Univ. Boulevard, St Louis, MO 63121-4499, USA. – S. C. Latta, Natl Aviary, Allegheny Commons West, Pittsburgh, PA 15212-5248, USA.

We compared the haemosporidian parasite faunas (*Plasmodium* and *Haemoproteus*) of small land birds on the islands of St Lucia, St Vincent and Grenada in the southern Lesser Antilles. The islands differ in distance from the South American source of colonists, proximity to each other, and similarity of their avifaunas. On each island, we obtained 419–572 blood samples from 22–25 of the 34–41 resident species. We detected parasite infection by PCR and identified parasite lineages by sequencing a portion of the mitochondrial cytochrome b gene. Parasite prevalence varied from 31% on St Lucia to 22% on St Vincent and 18% on Grenada. Abundant parasite lineages differed between the three islands in spite of the similarity in host species. As in other studies, the geographic distributions of the individual parasite lineages varied widely between local endemism and broad distribution within the West Indies, including cases of long-distance disjunction. St Vincent was unusual in the near absence of *Plasmodium* parasites, which accorded with low numbers of suitable mosquito vectors reported from the island. Parasites on St Vincent also tended to be host specialists compared to those on St Lucia and Grenada. Similarity in parasite assemblages among the three islands varied in parallel with host assemblage similarity (but not similarity of infected hosts) and with geographic proximity. Parasite prevalence increased with host abundance on both St Lucia and St Vincent, but not on Grenada; prevalence did not vary between endemic and more widespread host species. In addition, the endemic host species harbored parasites that were recovered from a variety of non-endemic species as well. These results support the individualistic nature of haemosporidian parasite assemblages in evolutionarily independent host populations.

Islands in the Lesser Antilles show unique relationships between birds and their haemosporidian parasites (*Plasmodium* spp. and *Haemoproteus* spp.) because of their isolation and independent coevolution between host and parasite populations (Fallon et al. 2003a, 2005, Svensson-Coelho and Ricklefs 2011). In particular, the prevalence of individual lineages of parasites on a particular host often varies between islands. A conspicuous example is the apparent absence of lineage OZ21 from bananaquits (*Coereba flaveola*) on the island of Martinique, in contrast to the consistently high prevalence of this parasite in bananaquits on other islands and, on Martinique, in other hosts, among them the Lesser Antillean bullfinch (*Loxigilla noctis*) (Apanius et al. 2000, Fallon et al. 2003a). Parasite lineages are named arbitrarily based on cytochrome b sequences, but they correspond to lineages identified in other studies from our laboratory. The general distribution of each parasite lineage, references, and GenBank accession numbers of associated cytochrome b sequences are provided in Appendix 2. Throughout this paper, *Plasmodium* lineages are indicated by bold type, *Haemoproteus* lineages of Columbiformes (subgenus *Haemoproteus*) by italic type, and *Haemoproteus* (*Parahaemoproteus*) lineages by normal type. Other distributional anomalies include distantly disjunct occurrences of some parasite lineages, such as OZ02, which is common in the Greater Antilles (except Jamaica) and the Yucatan Peninsula of Mexico, and was recovered from 5 individuals of four host species in Grenada, but not from the intervening islands (Fallon et al. 2005: lineage HH). Understanding patterns of parasite distributions, let alone explaining them, might be facilitated by examining sets of closely situated islands that have partially overlapping host faunas and perhaps different histories of association (Svensson-Coelho and Ricklefs 2011).

The southern islands of the Lesser Antilles – from north to south: St Lucia, St Vincent, and Grenada – present an opportunity to examine patterns of haemosporidian occurrence in more detail owing to the different mixtures of Antillean and South American influences on the avifaunas of these otherwise similar islands. Compared to the Lesser Antilles from St Lucia north, Grenada exhibits a relatively low prevalence of haemosporidian parasites in its avifauna, although the island also harbors several endemic lineages of parasite, at least within the context of the Lesser Antilles (Fallon et al. 2005). The striking differences between the haematozoan faunas of Grenada and St Lucia make the intervening island of St Vincent a favorable location for investigating the influence of history and geography on the

development of parasite communities. Fallon et al. (2005) commented on the relatively low parasite prevalence and low parasite diversity on St Vincent and Grenada, and the low sharing of parasite lineages between these islands. However, their conclusions were based on blood samples from only 81 small land-bird individuals obtained from St Vincent in 1993.

During April 2008, we revisited St Vincent and obtained 330 additional blood samples, bringing our sampling effort to a similar level across the three islands. We also produced 17 additional sequences for parasites from our 2002 Grenada samples. These new samples enable us to examine more closely the distributions of parasite lineages across the three islands and to determine whether these can be placed in a common framework of causation that includes differences in host faunas, variation in host genetic distance between island populations, and physical proximity of the islands. We also cannot overlook the potential role that vectors might play in haemosporidian distributions (Super and van Riper 1995, Nayar et al. 1998, Sol et al. 2000, Freed et al. 2005, Kilpatrick et al. 2006, Svensson-Coelho and Ricklefs 2011).

In this analysis, we compare the haemosporidian fauna of St Vincent with those of St Lucia and Grenada. We then ask whether similarity of island haemosporidian assemblages is related to 1) historical proximity between islands, 2) similarity of host species, and 3) genetic similarity between host populations on different islands. We also compared species lists of vectors on these islands to determine the extent to which haemosporidian assemblage similarity reflects the distribution of vectors. Finally, we ask whether the prevalence and diversity of parasites recovered from particular hosts can be related to host population size and endemism.

Material and methods

Islands and their avifaunas

Saint Lucia, St Vincent and Grenada are the major islands at the southern end of the Lesser Antilles volcanic arc (Fig. 1). They are oceanic islands without prior connection to each other or to continental land masses. Their subaerial history considerably predates the contemporary avifauna (Ricklefs and Bermingham 2008). The islands are similar in size, elevation, and habitat diversity (Ricklefs and Lovette 1999), as well as contemporary patterns of land use. Climates in the Lesser Antilles during glacial maxima are thought to have been cooler and drier than at present (Bonatti and Gartner 1973, Curtis et al. 2001). Lowland habitats of all three islands have been extensively transformed by agriculture and other development (Kimber 1988); however, each of the islands retains substantial areas of wet forest and cloud forest at higher elevations.

The avifauna of the Lesser Antilles has been derived primarily by colonization from both the south (continental South America) and the north (Greater Antilles; Ricklefs and Bermingham 2004, 2008). Colonists range from recent immigrants to old, genus-level endemics. Each of the islands harbors endemic species, such as the St Lucia black finch *Melanospiza richardsoni* on St Lucia, the whistling warbler *Catheropeza bishopi* and St Vincent parrot *Amazona guildingii* on St Vincent, and the Grenada dove *Leptotila wellsi* on Grenada. The permanent resident avifaunas

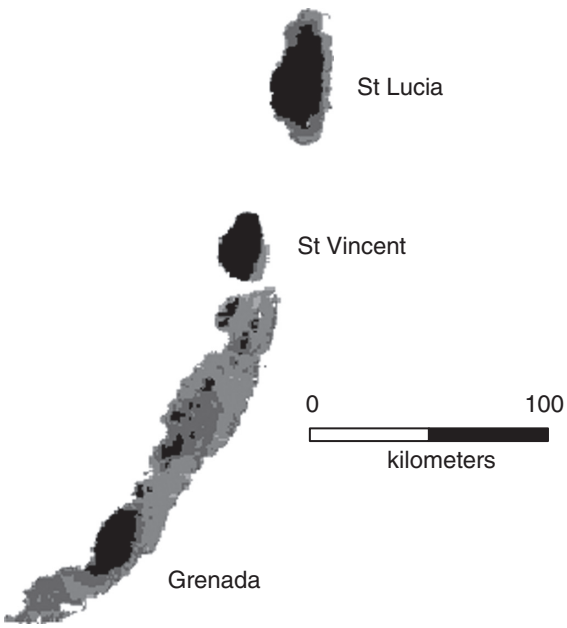

Figure 1. Map of the southern Lesser Antilles. Black areas are presently above water; the shaded areas indicate continental shelf at varying depths, which was mostly exposed during sea-level lows during the glacial maxima of the Pleistocene. Saint Lucia, St Vincent and Grenada have areas of 616, 350 and 310 km^2, respectively; elevation: 960, 1240, 840 m a.s.l.; habitat diversity (Simpson index of areas of five major habitat types): 3.08, 3.27, 3.26 (Ricklefs and Lovette 1999). Bathymetry data were reproduced from the GEBCO_08 Grid, ver. 20091120, <www.gebco.net>, and converted into an ascii file using GEBCO Grid Demonstrator ver. 2.13 (<www.bodc.ac.uk/products/software_products/gebco_grid_display/>). The final map was created in DIVA-GIS (<www.diva-gis.org/>).

comprise 41, 34, and 36 species, respectively, of which we sampled 25, 22, and 25 species. Saint Vincent and, especially, Grenada harbor populations of several South American species that have colonized the islands recently enough that they are undifferentiated (e.g. common ground dove *Columbina passerina*, shiny cowbird *Molothrus bonairiensis*, yellow-bellied elaenia *Elaenia flavogaster*, gray kingbird *Tyrannus dominicensis*, cocoa thrush *Turdus fumigatus*, and bare-eyed thrush *Turdus nudigenis*).

Sampling

We obtained the following blood samples from birds in representative habitats on each island: St Lucia (n = 222, Jul 1991; n = 197, Jul 2001), St Vincent (n = 81, May 1993, n = 330, Apr 2008), and Grenada (n = 98, Sep 1992, n = 474, Jun 2002). Lacking evidence of marked parasite faunal change over the period of the study (Fallon et al. 2004), samples from different years were combined for each island. All of the samples were obtained during the late spring and summer months, which include the early part of the rainy season in this region. In a Puerto Rican dry forest, samples of blood parasites obtained in Jan, May and Oct did not differ with respect to either overall prevalence or lineages of parasites (Fallon et al. 2004). Thus, even though samples were obtained at different times of the year on each island, we feel confident that this did not influence either prevalence or lineage type.

Blood samples (5–10 μL) were obtained by venipuncture from the brachial vein in the wing and stored in Puregene or Longmire's (Longmire et al. 1997) lysis buffer. All individuals were released immediately after processing (for further details of field methods, see Apanius et al. 2000, Fallon et al. 2003a, Latta and Ricklefs 2010). All samples were collected under IACUC protocols approved at the Univ. of Pennsylvania (1990s collections) and the Univ. of Missouri – St Louis (2000s collections), and under appropriate permits from the governments of St Lucia, St Vincent and the Grenadines, and Grenada.

Laboratory methods and phylogeny reconstruction

DNA was extracted from lysis buffer by alcohol precipitation following removal of proteins by ammonium acetate precipitation (Fallon et al. 2003a, 2005, Ricklefs et al. 2005). DNA samples were screened for the presence of haemosporidian parasites by PCR amplification of a 154 bp segment of the mitochondrial SSU ribosomal DNA (Fallon et al. 2003b). We amplified and sequenced regions of the mitochondrial cytochrome b gene from positive samples using a variety of primer pairs and methods (Fallon et al. 2005, Ricklefs et al. 2005, Latta and Ricklefs 2010, Outlaw and Ricklefs 2010). Our success in sequencing cytochrome b from infected individuals on Grenada was relatively low, possibly owing to poor quality of the extracted DNA, and so prevalence of some or all parasite lineages would be underestimated relative to the other islands. Moreover, our sequencing primers are not suitable for *Leucocytozoon* and so we cannot comment on the presence or absence of this related parasite. Sequences varying in length from 352 to 1100 bp, but mostly > 800 bp, were aligned in BioEdit and subjected to phylogenetic analysis using the RAxML black box (<http://phylobench.vital-it.ch/raxml-bb/index.php>) to produce bootstrapped maximum-likelihood trees with the default settings: a GTR plus gamma model of nucleotide substitution (Stamatakis 2006, Stamatakis et al. 2008).

Genetic distances between island populations of 10 common host species (*Coereba flaveola*, *Elaenia flavogaster*, *Elaenia martinica*, *Loxigilla noctis*, *Mimus gilvus*, *Myiarchus nugator*, *Tiaris bicolor*, *Tyrannus dominicensis*, *Turdus nudigenis* and *Vireo altiloquus*) were determined for two mitochondrial genes (ATPase6,8 [842 bp] and COI [648 bp]) for two individuals per population where available (unpubl.; Ricklefs and Bermingham 2001). Genetic distances were calculated in Phylip-3.69 (<http://evolution.genetics.washington.edu/phylip.html>) using the F84 model of sequence evolution with a transition/transversion ratio of 2.0 and a single rate of nucleotide substitution. Pooled within-population genetic distances ranged up to 0.006, and these were subtracted from the average distance between sequences from different islands to obtain a corrected interisland sequence divergence.

Assignment of *Plasmodium* and *Haemoproteus* lineages

Because no objective criteria exist to circumscribe independently evolving populations of parasites from single sequence data, we have designated lineages of parasites provisionally based on phylogenetic clustering and on both host and geographic distribution. Thus, genotypes that group phylogenetically and infect the same host species on a given island are considered to be a single lineage. Generally, genetic distances within designated lineages are 0.5% or less (Bensch et al. 2004), and among the haemosporidians of the southern Lesser Antilles genetic divergence is sufficient that lineages are distinctive (Fig. 2). Generic designation of each lineage was determined by comparison with published sequences (Perkins and Schall 2002, Ricklefs and Fallon 2002, Fallon et al. 2005, Martinsen et al. 2008).

Statistics

Prevalence of haemosporidians was compared among samples by G-test (Sokal and Rohlf 1995, p. 689 ff.). Other statistical tests are described in the results section.

Similarities between islands with respect to host species, infected hosts, and parasite lineages were quantified using Czekanowski's Index of Similarity (Magurran 1988)

$$C = \frac{\sum_{\text{species}} 2W}{\sum_{\text{species}} (A + B)},$$

where A and B are the number of samples of each host species or parasite lineage on each of two islands and W is the sum of the lesser of the numbers for each of the species. This index takes into account the relative abundances of each host in the sample.

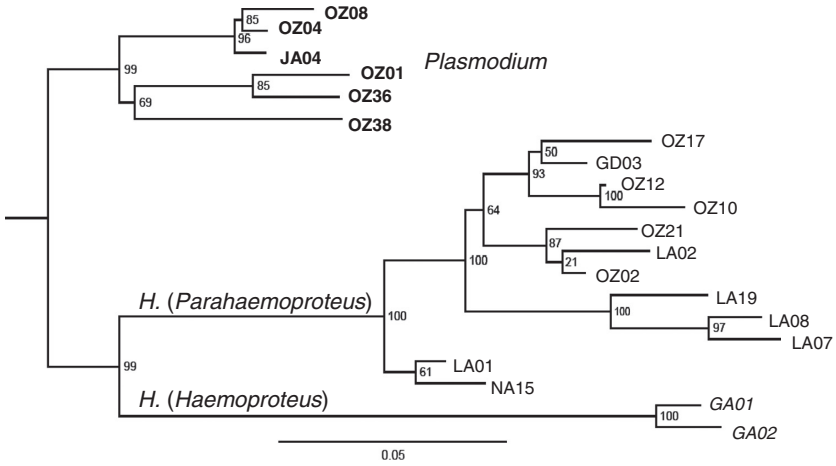

Figure 2. Phylogenetic relationships among the parasite lineages from St Lucia, St Vincent and Grenada based on cytochrome b sequences. The data were analyzed in RAxML using a GTR plus gamma model of nucleotide substitution. The scale bar represents 5% nucleotide substitution along a branch in the phylogeny. Small numbers at the nodes indicate bootstrap support. The lowermost clade includes the columbiform *Haemoproteus* (*Haemoproteus*), the middle clade consists of *Haemoproteus* (*Parahaemoproteus*), and the upper clade comprises *Plasmodium* spp.

Results

General overview of the host and parasite faunas

We obtained blood samples from 1402 individuals of 40 species of bird, of which 267 (17.7 ± 1.1%) yielded haemosporidian cytochrome b sequence (St Lucia: 419/25/118 [28.2 ± 2.2%]; St Vincent: 411/22/87 [21.2 ± 2.0%]; Grenada: 572/25/63 [11.0 ± 1.3%]). Prevalence of identified haemosporidian lineages, based on sequenced parasite cytochrome b, differed significantly among three islands ($G = 48.7$, $DF = 2$, $p < 0.0001$). Prevalence on St Vincent was marginally less than that on St Lucia ($G = 5.5$, $DF = 1$, $p = 0.02$), and prevalence on Grenada was significantly less than that on St Vincent ($G = 18.7$, $DF = 1$, $p < 0.0001$). Note, however, that sequences were obtained from slightly more than half the number of samples from Grenada that screened positive for infection (Fallon et al. 2005), whereas sequencing success was >90% on St Lucia and St Vincent. The cause of the lower sequencing success in the Grenada sample was not determined. When prevalence was based on positive screens (St Lucia 31%, St Vincent 22%, Grenada 18%), the islands still were significantly heterogeneous ($G = 21.2$, $p < 0.0001$), but St Vincent and Grenada did not differ ($G = 1.9$, $p = 0.17$).

Haemosporidian infections by species are presented in Appendix 1. Among the common host species sampled on two or more islands (Appendix 2), differences in prevalence of identified haemosporidian lineages between islands were driven primarily by the patterns in *Coereba flaveola* (SL [prevalence, 0.41] = SV [0.40] > GR [0.16]), *Loxigilla noctis* (SL [0.65] > SV [0.47] > GR [0.02]), *Margarops fuscus* (SL [0.60] > SV [0.00]), *Tiaris bicolor* (SL [0.56] > SV [0.10] > GR [0.03]), and *Vireo altiloquus* (SL [0.20] = SV [0.47] > GR [0.14]). None of the prevalence patterns significantly contradicted the trend SL > SV > GR. As in other studies, prevalence varied dramatically among species from more than 50% infected individuals in *Loxigilla noctis*, *Margarops fuscus* and *Tiaris bicolor* (on St Lucia) to none in reasonably large samples of *Geotrygon montana*, *Myiarchus nugator*, *Orthorhynchus cristatus* and *Tangara cucullata*.

The pattern of prevalence over the three islands was driven primarily by variation in three of the parasite lineages, **OZ04** being most abundant on St Lucia, OZ21 most abundant on St Vincent, but also common on St Lucia, and LA07 being most abundant on Grenada (Table 1). Except for the absence of LA02, a specialist on *Margarops* spp. in our sample, which is absent (apparently extinct, Bond 1956) from Grenada, none of the differences in recoveries among the islands was due to the absence of suitable hosts. For example, lineage OZ21, which is the most abundant haemosporidian in our West Indian samples and common on St Lucia and St Vincent, was recovered uniquely from a single individual of the hermit hummingbird *Glaucis hirsuta* on Grenada in spite of abundant suitable hosts, including *Coereba flaveola* and *Loxigilla noctis*.

The biogeographic position of parasite lineages recovered from St Vincent

Phylogenetically, the haemosporidian parasites recovered in this study fall into three clades: avian *Plasmodium*, *Haemoproteus* (subgen. *Haemoproteus*) and *Haemoproteus* (subgen. *Parahaemoproteus*) (Martinsen et al. 2008). *Haemoproteus* (*Haemoproteus*) occurs primarily in pigeons and doves (Columbidae). The subgenus is represented in this sample by two lineages (*GA01* and *GA02*) recovered in small numbers from *Columbina passerina* (Columbidae) on St Vincent and Grenada. Lineage *GA01* is broadly distributed in the Lesser Antilles and Greater Antilles, as well as in our samples from northern Venezuela and the Yucatan Peninsula of Mexico. *GA02* also is common in *C. passerina* on the Greater Antilles and in Mexico, and present but less common on other islands in the Lesser Antilles (Fallon et al. 2005: CPA1 and CPA2).

Six lineages of *Plasmodium* have been recovered from avian hosts in the southern Lesser Antilles: **JA04**, **OZ01**,

Table 1. Number of infected individuals recovered from each island for lineages with n ≥5. [a]Lineages of *Plasmodium* are indicated in bold type.

Lineage[a]	Number recovered per island			Remarks
	SL	SV	GR	
LA02	8	0	0	Common in *Margarops* spp., which were also sampled on St Vincent
LA07	2	6	28	Most common in *Coereba flaveola,* which was sampled in abundance on all the islands
LA08	6	0	0	Recovered mostly from *Loxogilla noctis,* which was sampled in abundance on all islands
OZ02	0	0	5	A host generalist
OZ04	29	0	4	Recovered primarily from *C. flaveola, L. noctis,* and *Tiaris bicolor,* which were common on all islands
OZ10	2	7	0	Only from *Vireo altiloquus,* sampled most commonly on St Lucia
OZ21	49	62	1	Recovered primarily from *C. flaveola* and *L. noctis,* which were also common on Grenada

OZ04, **OZ08**, **OZ36** and **OZ38**. The absence of all but one of these lineages from St Vincent is striking. The only *Plasmodium* lineage recovered from St Vincent was **OZ38** from single individuals of *Loxigilla noctis* and *Tyrannus dominicensis*.

JA04 appears to be an extreme geographic disjunct, with 3 examples obtained from *Elaenia martinica* on St Lucia and additional ones from Trinidad/Venezuela (*Elaenia flavogaster*, *Quiscalus lugubris* and *Troglodytes aedon*), 1 from Yucatan (*Mimus gilvus*), and 7 from six different hosts on Jamaica. Although not statistically significant, the absence of this parasite from 9 *E. martinica* on St Vincent and 33 *E. flavogaster* on St Vincent and Grenada is consistent with the general paucity of *Plasmodium* parasites on these islands compared to St Lucia. **OZ01** (lineage PA in Fallon et al. 2005) has been recovered from 84 samples altogether, distributed among a variety of hosts from the Greater Antilles through the Lesser Antilles and including one example from Trinidad, plus widespread distribution in North America and the Yucatan Peninsula.

The absence of the common **OZ04** (PC in Fallon et al. 2005) from St Vincent (and only 4 from Grenada) is striking considering the 29 examples from a variety of common host species on St Lucia. We have recovered almost 200 of these parasites, particularly from Jamaica and the Lesser Antilles, including three from Trinidad. Clearly, however, the lineage is rare south of St Lucia. *Plasmodium* lineage **OZ36** apparently specializes on the host genus *Vireo*. It was recovered from three *V. altiloquus* from St Lucia, and otherwise from Missouri (1 *V. olivaceus*) and the Yucatan Peninsula (2 *V. magister* and 2 *V. griseus*). Considering the large number of *Vireo* samples in our collections from throughout the Caribbean Basin, **OZ36** appears to have a highly disjunct distribution. *Plasmodium* lineage **OZ38**, recovered from two individuals (*Loxigilla noctis* and *Tyrannus dominicensis*) on St Vincent, has otherwise been found only in a white-eyed vireo *V. griseus* from Missouri, a wintering blackpoll warbler *Dendroica striata* from Puerto Rico, and single individuals of the yellow oriole *Icterus nigrogularis* and the rufous-and-white wren *Thryothorus rufalbus* on Trinidad.

Striking disjunctions also occur among lineages of *Haemoproteus* (*Parahaemoproteus*). For example, LA01 (HF) and LA02 (HG) are restricted to host species in the family Mimidae, primarily from the islands of Montserrat, Guadeloupe, and St Lucia, although suitable hosts occur on intervening islands (Dominica and Martinique) and on St Vincent (*Margarops fuscus*), and LA01 is known from *Mimus gilvus* in Venezuela and *Dumatella carolinensis* sampled in Connecticut and Alabama (Fallon et al. 2005, unpubl.). Another remarkable case is OZ02 (HH), with over 200 examples from the Greater Antilles, the Yucatan Peninsula, and North America, and 5 highly disjunct examples from four disparate host species on Grenada (*Glaucis hirsuta*, *Troglodytes aedon*, *Mimus gilvus* and *Turdus nudigenis*). This parasite is 2.6% cytochrome b divergent from OZ21 in a large clade with other sequences recovered from North America (Ricklefs et al. 2005). Equally surprising is the absence of the abundant and widespread OZ21 (HC, *Haemoproteus coatneyi*, Svensson and Ricklefs 2009) from Grenada (save 1 example from *Glaucis hirsuta*), where it is apparently replaced by LA07 (HD), the commonest parasite of *Coereba flaveola* on that island. NA15, recovered from a single *Turdus fumigatus* on St Vincent, has otherwise been seen by us only from one individual of *Turdus migratorius* in Missouri.

The most common lineage on St Vincent is OZ21 (HC), which is a common parasite among a variety of passerines with many examples from Puerto Rico to St Lucia, as well as a number of North American passerines. OZ21 is identical to OZ07, which is common in myrtle warblers *Dendroica coronata* sampled in Michigan and Connecticut. OZ21 was the most common infection reported in 1993 on St Vincent (6 of 13 infections) (Fallon et al. 2005). Another common lineage on St Vincent is LA07, which occurs primarily in bananaquits through the Lesser Antilles to Puerto Rico and Hispaniola.

Five sequences obtained from black-whiskered vireos *Vireo altiloquus* on St Vincent were allied with OZ10 (HB), which has been recovered almost exclusively from red-eyed vireos *V. olivaceus* in the Ozark Mountains of Missouri; the related OZ12 (two examples from St Vincent) is relatively common in *V. altiloquus* in the West Indies, but including records from *V. olivaceus* from Missouri and northern Venezuela. The St Lucia OZ12 sequences were also recovered from black-whiskered vireos. Another related sequence (SV157, *V. altiloquus*) belongs to lineage GD03, which was also recorded from Grenada in one individual each of *Elaenia flavogaster*, *Glaucis hirsute* and *V. altiloquus*; *Tiaris olivacea* from the Cayman Islands; *Buteo lineatus* from North Carolina; *Dendroica magnolia* wintering on the Yucatan Peninsula; and as lineage LA26 from 4 *V. olivaceus* in Trinidad.

The picture that emerges from distributions of many parasite lineages in the West Indies is one of extreme idiosyncrasy, with indications either of long-distance

dispersal, local extinction of parasite lineages from individual islands, or both. Host distributions are less likely to play a role in the presence of parasites because most common host species are widespread throughout the Lesser Antilles. Variations in vector distribution are also a possibility, but we do not know the particular vectors of the Haemosporida surveyed in this study.

Host specialization

Many of the haemosporidian lineages on St Lucia and Grenada were recovered from several host species, up to 7 in the case of OZ21 on St Lucia and 8 in the case of LA07 on Grenada. Number of hosts tends to increase with sample size, as one would expect (Fig. 3), however lineages on St Vincent consistently were recovered from fewer hosts than on the other islands, OZ21 being the only lineage appearing in more than one host species.

General patterns

We ask whether the similarity of island haemosporidian communities is related to 1) the historical proximity between the islands, 2) the similarity of host communities, 3) the genetic similarity between host populations on different islands, and 4) the similarity of the potential vector communities. We calculated the parasite lineage similarity between the islands on the basis of relative abundance (C) and presence/absence (Sørensen's index S) (Table 2). The C-index shows that parasite similarity is greater between St Lucia and St Vincent (0.55) than it is between either of these islands and Grenada (0.14 and 0.19), respectively. This pattern follows closely that of the most abundant parasite lineage (OZ21), which is common on both St Lucia and St Vincent, but practically absent from Grenada. Considering solely presence and absence (S), parasite lineage similarity is greater between St Vincent and Grenada (0.56) than it is between these islands and St Lucia (0.27, 0.36).

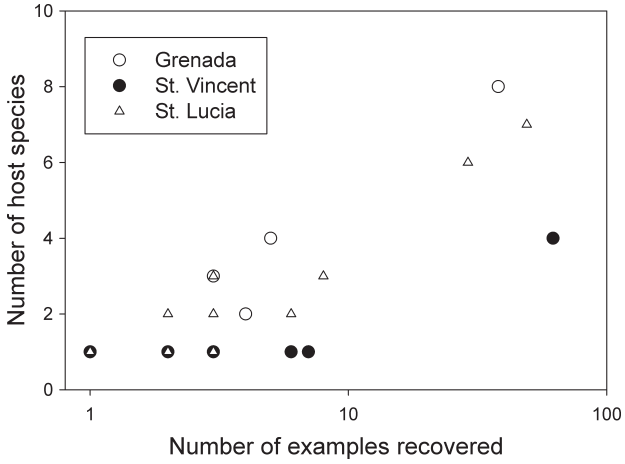

Figure 3. Number of host species for each named (non-unique) parasite lineage on St Lucia, St Vincent and Grenada as a function of the sample size (total number of infections per island). The number of singleton infections recovered (one example from one host) was 3 on Grenada, and 2 each on St Vincent and St Lucia.

Island proximity

The historical proximity of St Vincent and Grenada is apparent in the relatively high host similarity and lack of host genetic differentiation between the islands (below). This is also reflected in the similarity of the parasite lineages based on presence/absence (S). Lineage similarity based on parasite relative abundance is low owing to the relatively low prevalence of sequenced parasites on Grenada (11% compared to 21% on St Vincent and 28% on St Lucia). Thus, the difference between the parasite communities in these otherwise similar host communities reflects differences in prevalence rather than parasite lineages.

Host community similarity

We estimated host community similarity on the basis of both presence/absence (S) and relative abundance (C). Although sample sizes are not equivalent to host population estimates, they match more subjective impressions of abundance for most species and were used in this analysis as proxies for host abundance. Potential hosts, in this case all the species in our samples but not including unsampled species, are more similar between St Vincent and Grenada, whether by C or S (0.62, 0.72), than hosts on either island are to St Lucia (SV: 0.49, 0.55; GR: 0.33, 0.16). Similarities among infected host species are not so well differentiated (i.e. similarities are somewhat higher: 0.40–0.74) and favor a closer connection between St Lucia and St Vincent for C and between St Lucia and Grenada for S. The parasite connection between St Lucia and St Vincent is based on infections of *Coereba flaveola*, *Loxigilla noctis*, *Tiaris bicolor* and *Vireo altiloquus*. The only close similarity of infected hosts between St Vincent and Grenada is due to *C. flaveola*, although only 6 of 41 infected bananaquits on St Vincent harbored the common parasite lineage on Grenada (LA07).

Genetic differentiation of host populations

Host taxa were undifferentiated between St Vincent and Grenada. Moderate to strong genetic breaks distinguish populations of *Coereba flaveola* (0.7%), *Loxigilla noctis* (0.5%), and *Vireo altiloquus* (3.8%) on St Lucia and St Vincent (Ricklefs and Bermingham 2001), suggesting separation on the order of 10^5 to 10^6 yr, or more (Weir and Schluter 2008). All other potential host populations for which we have sequences were undifferentiated across the islands.

The difference between parasite communities on St Lucia and St Vincent is associated with genetic differentiation between island populations of two of the most important host species (*Loxigilla noctis* and *Coereba flaveola*), but the parasites of these species do not differ consistently between these islands. The predominant parasite of *L. noctis* (OZ21) is the same on both islands. However, although *C. flaveola* also is infected by this parasite on both islands, the predominant parasite lineage of this host on St Lucia is **OZ04**, which belongs to the genus *Plasmodium*. This parasite also infects *Tiaris bicolor* on St Lucia, but the St Vincent populations of *T. bicolor*, like

Table 2. Between-island comparisons of parasite lineages, host species, mosquito species, geographic distance, and genetic distances. Similarity indices between islands are based on both presence/absence data (S) and relative abundance (C). Genetic distances are negligible (0%), low (<1%), or high (>1%).

	SL–SV	SV–GR	SL–GR
Parasite lineages (C)	0.546	0.187	0.144
Parasite lineages (S)	0.273	0.556	0.364
All hosts (C)	0.487	0.619	0.327
All hosts (S)	0.553	0.723	0.163
Infected hosts (C)	0.742	0.547	0.556
Infected hosts (S)	0.444	0.400	0.667
Proximity	Medium	High	Low
Mosquito species (C)	0.215	0.509	0.702
Mosquito species (S)	0.353	0.541	0.553
Genetic distances	Negl. (5/8) Low (2/8) High (1/8)	Negl. (6/6)	Negl. (4/6) Low (1/6) High (1/6)

those of *C. flaveola*, harbor OZ21, even though the *Tiaris* populations on the two islands are undifferentiated.

Although host populations are not genetically differentiated between St Vincent and Grenada, their parasites differ in several cases. Thus, *Vireo altiloquus* from Grenada is distinguished by a low level of infection (1 of 7 individuals) compared to St Vincent (9 of 19; $G = 10.2$, $DF = 1$, $p = 0.0015$), and notably the absence of the *Vireo*-specific lineage OZ10 from Grenada. Other examples of dramatic differences in parasites on hosts, such as *Loxigilla noctis* between St Vincent (22/47) and Grenada (1/43) ($G = 27.2$, $DF = 1$, $p < 0.0001$), and *Coereba flaveola* between St Vincent (41/102) and Grenada (33/207) ($G = 20.9$, $DF = 1$, $p < 0.0001$), also are not associated with conspicuous genetic breaks. In the case of *Margarops fuscus* between St Lucia (12/20) and St Vincent (0/9) ($\chi^2 = 6.9$, $DF = 1$, $p = 0.009$), we lack genetic data from both host populations (Hunt et al. 2001).

The potential vector communities

Collections of mosquitoes from the southern Lesser Antilles have been described by Belkin and Heinemann (1976). We consider these collections to be representative of the potential vector assemblages on each of the islands, at least from the standpoint of calculating community similarity. For all species of Culicidae, the samples from St Lucia and Grenada have the highest similarity, particularly accounting for relative abundance (C); St Lucia and St Vincent are least similar by both C and S indices (Table 2). Patterns of mosquito communities thus do not match the pattern of haemosporidian communities overall.

Although the vectors of the parasite lineages recovered in this study are unknown, mosquitoes are believed to transmit only *Plasmodium*, and this primarily by species in the genera *Culex*, *Aedes* and *Culiseta*, with evidence for a few species of *Anopheles*, *Psorophora* and *Mansonia* being competent vectors (Valkiunas 2005). Collections of species in these genera (*Mansonia* and *Culiseta* were not listed from the islands) numbered 229 (80% of the total) on St Lucia and 201 (72%) on Grenada, but only 23 (27%) on St Vincent. Considering only *Culex* and *Aedes*, the percentages were 61, 46 and 21%, respectively. The St Vincent sample was collected during November and December, while collections on the other islands were primarily from July. However, both July and October collections were made on Grenada, and the two differed little (81 and 66% competent genera). The absence of abundant potential vectors of *Plasmodium* on St Vincent corresponds strikingly with the absence of *Plasmodium* lineages from the island (2 of 87 [2%] infections in 411 [<1%] potential hosts), however Grenada also lacked many cases of *Plasmodium* infection (5 of 63 [8%] infections in 572 [1%] potential hosts) compared to St Lucia (38 of 118 [32%] in 411 [9%] potential hosts). A few species of mosquito present commonly on St Lucia were absent from both St Vincent and Grenada: *Aedes tortilis*, *Culex coronator*, *C. declarator* and *C. bisulcatus*, and so it remains possible that variation in *Plasmodium* infection among the islands results from differences in the vector communities.

Host characteristics

Because haemosporidian prevalence varies so much between populations of the same host on different islands, it is unlikely that infection by haemosporidians is related to traits of species, such as body size, plumage coloration, diet, and feeding stratum. In other community-level analyses of haemosporidian infection, we have failed to find such correlations (Scheuerlein and Ricklefs 2004, Ricklefs et al. 2005). The unique outcomes of host–parasite coevolutionary interactions within individual island populations suggests, however, that the host distribution of avian haemosporidian parasites might be influenced by genetic factors controlling disease resistance (Fallon et al. 2003a, this paper). Although individual ecological and behavioral traits might not influence parasite diversity or prevalence on a particular host, it is possible that parasite infection might reflect population characteristics, particularly the absolute size and density of hosts. The only indicator of host population characteristics in this study is the size of the sample of captured birds.

Population size

We compared the number of infected and uninfected individuals for the more common species (those together comprising more than half the sample) and the less common species on each of the islands (Table 3). The more common species had significantly higher parasite prevalence on St Lucia and St Vincent, but not on Grenada.

Endemism in the West Indies

We contrasted infection rates between host species that are endemic to the West Indies and those whose distributions also extend to the mainland (Table 4). The non-endemic species are primarily recent colonists from northern South America (Ricklefs and Bermingham 2008), although, at least in the bananaquit *Coereba flaveola*, continental and West Indian populations have had a long history of separation (Bellemain et al. 2008). West Indian endemics make up the majority of the species and individuals sampled

Table 3. G-tests of the association between haemosporidian infection and the relative abundance of the host population. The 3 or 4 most abundant species on each island (comprising more than half the individuals) were contrasted with the less common species.

		Individuals			
	Species	Not infected	Infected	G (adj)	p
St Lucia					
Upper half	4	141	88	27.2	< 0.0001
Lower half	21	160	30		
St Vincent					
Upper half	3	157	71	32.7	< 0.0001
Lower half	19	167	16		
Grenada					
Upper half	3	256	37	1.6	0.21
Lower half	22	253	21		

on St Lucia; they are about equally balanced with non-endemics on St Vincent, and are the minority of species and individuals on Grenada. The prevalence of haemosporidians did not differ between endemic and non-endemic species on St Lucia ($G = 0.26$, $p = 0.61$) or St. Vincent ($G = 2.35$, $p = 0.13$), but infections were more common in non-endemic species on Grenada ($G = 19.4$, $p < 0.0001$), although this result depends solely on the high prevalence of parasites in *C. flaveola* and thus is ambiguous.

Discussion

Temporal change in haemosporidian communities

The 1993 samples from St Vincent were so few that no significant changes in the parasite fauna were detected between the earlier sample and 2008. However, one coincidental change is worth noting. Lineage LA08 (HE) was recorded from St Lucia in 1991, but not in 2000. Hence, its absence from the 2008 St Vincent samples might represent a similar disappearance of the lineage from the island. The lineage is practically endemic to *Loxigilla noctis*, which is abundant on both islands, as well as on Grenada, where the lineage did not appear either in the small 1992 sample or in the much larger 2002 sample. Although these observations are suggestive of changes in parasite assemblages over periods on the order of a decade, more comprehensive collections repeated at long intervals would be needed to provide a detailed appraisal of parasite dynamics over this time scale. Nevertheless, haemosporidian assemblages undoubtedly have a dynamic aspect that cannot be ignored. Moreover, as pointed out by Fallon et al. (2003a, 2004, 2005), replacements of haemosporidian lineages in host populations across islands and over time are consistent, in some cases, with dynamic interactions of lineages within host populations and between host species.

Parasite distributions

We found substantial variation in the distributions of parasite lineages among the three islands that were independent of differences in available hosts, which in any case were minor for the most abundant host species on the islands. Differences in parasite prevalence and lineage identity within particular host populations were not associated with mitochondrial genetic differentiation between island populations, which were small or absent for most of the abundant host species. Based on presence/absence, parasite lineage assemblages were more similar on St Vincent and Grenada than they were between these islands and St Lucia. This is in accord with the geographic proximity of the islands, which were nearly connected during Pleistocene glacial sea-level lows. Based on relative abundance, however, the parasite assemblages of St Lucia and St Vincent were more similar, largely because of the predominance of a single lineage (OZ21) on both islands.

The host communities were most similar between St Vincent and Grenada, whether judged by presence/absence or relative abundance. The range of potential hosts on Grenada exhibited distinct differences from those on St Lucia, owing to the presence of several South American species, although the major hosts on St Lucia (*Coereba flaveola*, *Loxigilla noctis*, *Tiaris bicolor* and *Vireo altiloquus*)

Table 4. G-tests of the association between haemosporidian infection and the endemicity status of the host population.

		Individuals			
	Species	Not-infected	Infected	G (adj)	p
St Lucia					
Endemic	17	239	91	0.26	0.61
Non-end	8	62	27		
St Vincent					
Endemic	12	145	31	2.3	0.12
Non-end	10	179	56		
Grenada					
Endemic	8	151	4	19.4	< 0.0001
Non-end	17	358	59		

also occurred commonly on Grenada. Parasite distributions emphasize the idiosyncrasy of occurrences, undoubtedly to some extent reflecting unique outcomes of parasite–host coevolutionary interactions.

The most abundantly parasitized species on Grenada was *Coereba flaveola*, which harbored primarily lineage LA07, which otherwise is most common in the Greater Antilles and only sporadically distributed in the Lesser Antilles, while being relatively common in samples from Trinidad and northern Venezuela (Fallon et al. 2005). In addition to LA07, eight additional non-unique lineages were found in the Grenada sample. Most of these were also recorded from St Vincent, St Lucia, or other islands in the Lesser Antilles (Fallon et al. 2005). Lineage OZ02 (HH) is noteworthy, however, in that this parasite has been reported commonly from North America, Hispaniola and Puerto Rico in the Greater Antilles, and from Grenada. We have not recorded this lineage from elsewhere in the Lesser Antilles or from Trinidad and northern Venezuela. The parasite appears to be a host generalist wherever it occurs, including Grenada.

It seems unlikely that the uniqueness of the parasite assemblage on Grenada is related to its proximity to South America. The proportion of non-endemic host species and individuals was highest in the Grenada sample, followed by St Vincent and St Lucia. Fallon et al. (2005) identified more parasite lineages shared between northern South America and St Lucia, but not recorded from Grenada and St Vincent (OZ17 [lineage HA of Fallon et al. (2005)], LA08 [HE], LA01 [HF], *P. elongatum*, **OZ01** [PA], **OZ36** [PB]) than were shared between northern South America and Grenada and St Vincent, but not St Lucia ([HU1], *GA01* [Cpa1], *GA02* [Cpa2]). Thus, we find little evidence that the special host fauna of Grenada, resulting from its proximity to South America, has influenced its haemosporidian fauna.

Host specialization

In spite of similar numbers of potential host species on St Vincent, parasite lineages individually infected fewer host species than on either St Lucia or Grenada. This partly reflects the narrow range of parasite lineages because two lineages (*GA01*, $n = 2$; *GA02*, $n = 3$) are almost totally restricted to a single host (*Columbina passerina*) wherever they occur, and OZ10 ($n = 7$) is virtually restricted to *Vireo* spp. Nonetheless, LA07 was recovered only from *Coereba flaveola* ($n = 6$) on St Vincent, whereas it appeared in 8 host species on Grenada. The most abundant parasite on St Vincent (OZ21, $n = 62$) was recovered from 4 hosts, but 49 examples from St Lucia came from 7 host species. Thus, the tendency of parasite lineages to specialize with respect to hosts on St Vincent appears to represent a real phenomenon. The diversity of hosts and parasites on St Lucia and St Vincent varied in parallel (Table 5), and so the relative accessibility of parasite lineages to hosts also cannot explain the difference in host specialization. St Vincent lacked *Plasmodium* spp. lineages of parasites (except for two examples of **OZ38**), potentially owing to the paucity of suitable vectors. The diversity of mosquito species on the island also is low compared to St Lucia and Grenada (Belkin and Heinemann 1976), suggesting that species of ceratopogonid vectors of *Haemoproteus* spp. might also be few, and potentially limit host breadth. Clearly, the role of vectors in parasite specialization would be a fruitful avenue for future work.

Table 5. Diversity of host species and parasite lineages. Diversity is presented as the Simpson index, $D = 1/\Sigma p_i^2$, where p_i is the proportion of individuals or infections in the *i*th species or lineage.

Simpson index (D)	St Lucia	St Vincent	Grenada
Host	10.140	7.903	6.265
Parasite	4.409	3.239	3.372
Ratio	0.435	0.410	0.538
Mosquito species	12.95	5.78	13.8

Host abundance

One of the striking results of our analyses was the positive association between host abundance and parasite prevalence (Table 3). This pattern is consistent with the hypothesis that infections spread more readily in dense host populations (Anderson and May 1979, 1981, but see Begon et al. 1999), assuming that captures are roughly proportional to host density (Blake and Loiselle 2001, Derlindati and Caziani 2009). There was no relationship between host abundance on a particular island and the diversity (D) of parasite lineages recovered from that host (all $p > 0.05$), and so the increasing parasite prevalence as a function of host abundance reflects the prevalence of individual parasite lineages and not diversity of lineages among infections.

Host history and endemism

We found no evidence that haemosporidians are more or less frequent in populations of West Indian endemics than they are among continental hosts that have spread recently to the islands. The endemic lineages also have varied histories, some of them being endemic to individual islands with no evidence of recent dispersal, while others, judging from phylogeographic relationships, have spread more recently among the islands (Ricklefs and Bermingham 2004). In the present sample of species from the southern Lesser Antilles, we captured small numbers of individuals from a variety of single-island endemics or endemic species that are highly differentiated among islands and represent old, long-isolated populations. These species included *Leptotila wellsi*, *Troglodytes aedon* and *Tangara cucullata* on Grenada, *T. aedon* and *Catheropeza bishopi* on St Vincent, and *Contopus laterostris*, *Dendroica adelaidae* (Lovette et al. 1998), *Icterus laudabilis* (Lovette et al. 1999), *Melanospiza richardsoni* and *Ramphocinclus brachyurus* (Hunt et al. 2001) on St Lucia. Counting all infections for which we obtained sequences, the prevalence of parasites was significantly lower in the old island ($7/93 = 7.5\%$) endemics than in the more recently expanded populations lacking differentiation between islands ($261/1309 = 19.9\%$) ($G = 10.4$, $DF = 1$, $p = 0.001$). The 7 parasite lineages recovered from the single-island-endemic host populations represented common parasites on the respective islands.

This result suggests a general connection between the long-term histories of populations on islands and their

haemosporidian parasites. However, the island-endemic host populations comprised small samples on average (5–19 individuals), and the association between-island endemism and parasite prevalence might simply represent the effect of host abundance. We therefore compared the prevalence of haemosporidians in island-endemic host populations ($n = 10$) and in non-endemic host populations having samples between 5 and 19 individuals ($n = 23$). The prevalence among the less common non-endemic hosts (37/263 = 14.1%) was only marginally higher than in the endemic hosts ($G = 2.9$, $DF = 1$, $p = 0.087$).

If this result reflects the history of island populations, its meaning is unclear. Island endemic species are thought to be more susceptible to invasive pathogens (van Riper et al. 1986), but evidence of weakened immune responses in island bird populations is equivocal (Matson 2006, Beadell et al. 2007, Matson and Beadell 2010). It is possible that island-endemic bird populations have gone through population bottlenecks in the past during which they have lost host-specific or even generalist lineages, but we have no evidence from host genetic diversity bearing on this point. Island endemics also tend to have restricted ecological distributions shifted towards forested habitats at higher elevations; all the infections recovered from island endemics involved species with distributions extending to low elevation and including secondary forest or open dry forest. Thus, it is also possible that the lower parasite prevalence in these species is associated with their distribution on islands primarily at higher elevations. However, parasite prevalence in a forested location on St Vincent at 325 m a.s.l. (25 of 70, or 35.7%) significantly ($p < 0.01$) exceeded that at lower, more coastal sites (40 of 209, or 19.1%); prevalence in an abandoned orchard at 499 m a.s.l. was 13 of 55 (23.6%). Thus, even though most of the species were the same at high and low elevations, parasite prevalence did not appear to decrease with increasing elevation.

Vector communities

The near absence of *Plasmodium* on St Vincent clearly was not due to the absence of suitable host populations for the four *Plasmodium* parasites present on St Lucia and Grenada, but published information on mosquito samples suggested that potential vectors of *Plasmodium* might have been relatively less common on the island. The absence of suitable vectors can influence the prevalence of haemosporidian parasites (Super and van Riper 1995, Freed et al. 2005). However, without more detailed information on vector abundance and feeding patterns, little more can be said about this.

As in other analyses of haemosporidian parasites in the Lesser Antilles (Fallon et al. 2003a, 2005, Svensson-Coelho and Ricklefs 2011), the distribution of parasite lineages across St Lucia, St Vincent, and Grenada was highly idiosyncratic, even among host populations of the same species. This is consistent with the idea that host–parasite interactions evolve rapidly and can produce substantially different outcomes on different islands. The absence of endemic lineages of parasites in endemic host populations of birds on each of the islands is also consistent with the dynamic nature of haemosporidian–host interactions; the host–parasite relationships simply evolve too rapidly to establish long-term associations. The distributions also indicate potential interactions between parasite lineages, particularly with respect to the apparent replacement of the common *Haemoproteus* lineage OZ21 with *Haemoproteus* lineage LA07 on Grenada. The absence of the common *Plasmodium* lineage **OZ04** from both St Vincent (where other *Plasmodium* lineages are mostly absent) and Grenada also is puzzling, but we did not identify a potential competing parasite lineage on either island.

The lower parasite prevalence on St Vincent and Grenada compared to St Lucia is enigmatic, particularly as the difference appeared in hosts that occurred on all three islands. Although Grenada and St Vincent have a distinctly South American influence in their avifaunas, parasite prevalence did not differ significantly between endemic host species in the Lesser Antilles and recent colonists from South America. Additional comparative analyses of haemosporidian parasite distributions might help to refine some of the patterns identified in this study, but it is also clear that many issues will not be resolved without experimental studies of susceptibility to infection across host species and islands and without analyses of the biting patterns and competences as hosts on the part of dipteran vectors. The strongest generalization to come from this study concerns the evolutionary lability of host–parasite interactions combined with the unique outcomes of host–parasite coevolution on different islands.

Acknowledgements – We thank Julie Hart, Chris Brown, Dave Ziolkowski, Jr and Michael Phillip for assistance in the field; Bradford B. Latham, Donald Ellis, and Amos Glasgow, Forestry Dept, Saint Vincent and the Grenadines, for assistance in the field and for sharing their knowledge of the local avifauna; Birdie Delves and Owen Delves for permission to work on their properties in St Vincent; Brian Johnson, Director of Forestry, St Vincent and the Grenadines, for permits to collect blood samples, and for encouragement and support; Alan Joseph, Chief Forestry Officer, Grenada, for field research permits; and Alan Joseph, Edward Massiah, and Bonnie Rusk for logistical advice. The Curators of the Univ. of Missouri provided financial support.

References

Anderson, R. M. and May, R. M. 1979. Population biology of infectious diseases: part I. – Nature 280: 361–367.

Anderson, R. M. and May, R. M. 1981. The population dynamics of microparasites and their invertebrate hosts. – Phil. Trans. R. Soc. B 291: 451–524.

Apanius, V., Yorinks, N., Bermingham, E. and Ricklefs, R. E. 2000. Island and taxon effects in parasitism and resistance of Lesser Antillean birds. – Ecology 81: 1959–1969.

Beadell, J. S. and Fleischer, R. C. 2005. A restriction enzyme-based assay to distinguish between avian hemosporidians. – J. Parasitol. 91: 683–685.

Beadell, J. S., Ishtiaq, F., Covas, R., Melo, M., Warren, B. H., Atkinson, C. T., Bensch, S., Graves, G. R., Jhala, Y. V., Peirce, M. A., Rahmani, A. R., Fonseca, D. M. and Fleischer, R. C. 2006. Global phylogeographic limits of Hawaii's avian malaria. – Proc. R. Soc. B 273: 2935–2944.

Beadell, J. S., Atkins, C., Cashion, E., Jonker, M. and Fleischer, R. C. 2007. Immunological change in a parasite-impoverished

environment: divergent signals from four island taxa. – PLoS One 2: e896.
Begon, M., Hazel, S. M., Baxby, D., Bown, K., Cavanagh, R., Chantrey, J., Jones, T. and Bennett, M. 1999. Transmission dynamics of a zoonotic pathogen within and between wildlife host species. – Proc. R. Soc. B 266: 1939–1945.
Belkin, J. N. and Heinemann, S. J. 1976. Collection records of the project ''Mosquitoes of middle America'' 6. Southern Lesser Antilles: Barbados (BAR), Dominica (DOM), Grenada (GR, GRR), St Lucia (LU), St Vincent (VT). – Mosquito Syst. 8: 237–297.
Bellemain, E., Bermingham, E. and Ricklefs, R. E. 2008. The dynamic evolutionary history of the bananaquit (*Coereba flaveola*) in the Caribbean revealed by a multigene analysis. – BMC Evol. Biol. 8: 240.
Bensch, S., Perez-Tris, J., Waldenstrom, J. and Hellgren, O. 2004. Linkage between nuclear and mitochondrial DNA sequences in avian malaria parasites: multiple cases of cryptic speciation? – Evolution 58: 1617–1621.
Blake, J. G. and Loiselle, B. A. 2001. Bird assemblages in second-growth and old-growth forests, Costa Rica: perspectives from mist nets and point counts. – Auk 118: 304–326.
Bonatti, E. and Gartner, S. Jr 1973. Caribbean climate during Pleistocene ice ages. – Nature 244: 563–565.
Bond, J. 1956. Checklist of birds of the West Indies. – Acad. Nat. Sci.
Curtis, J. H., Brenner, M. and Hodell, D. A. 2001. Climate change in the circum-Caribbean (Late Pleistocene to Present) and implications for regional biogeography. – In: Woods, C. A. and Sergile, F. E. (eds), Biogeography of the West Indies. Patterns and perspectives. CRC Press, pp. 35–54.
Derlindati, E. J. and Caziani, S. M. 2009. Using canopy and understory mist nets and point counts to study bird assemblages in Chaco forests. – Wilson Bull. 117: 92–99.
Escalante, A. A., Freeland, D. E., Collins, W. E. and Lal, A. A. 1998. The evolution of primate malaria parasites based on the gene encoding cytochrome b from the linear mitochondrial genome. – Proc. Natl Acad. Sci. USA 95: 8124–8129.
Fallon, S. M., Bermingham, E. and Ricklefs, R. E. 2003a. Island and taxon effects in parasitism revisited: avian malaria in the Lesser Antilles. – Evolution 57: 606–615.
Fallon, S. M., Ricklefs, R. E., Swanson, B. L. and Bermingham, E. 2003b. Detecting avian malaria: an improved polymerase chain reaction diagnostic. – J. Parasitol. 89: 1044–1047.
Fallon, S. M., Ricklefs, R. E., Latta, S. and Bermingham, E. 2004. Temporal stability of insular avian malarial parasite communities. – Proc. R. Soc. B 271: 493–500.
Fallon, S. M., Bermingham, E. and Ricklefs, R. E. 2005. Host specialization and geographic localization of avian malaria parasites: a regional analysis in the Lesser Antilles. – Am. Nat. 165: 466–480.
Freed, L. A., Cann, R. L., Goff, M. L., Kuntz, W. A. and Bodner, G. R. 2005. Increase in avian malaria at upper elevation in Hawai'i. – Condor 107: 753–764.
Hunt, J. S., Bermingham, E. and Ricklefs, R. E. 2001. Molecular systematics and biogeography of Antillean thrashers, tremblers, and mockingbirds (Aves: Mimidae). – Auk 118: 35–55.
Kilpatrick, A. M., Kramer, L. D., Jones, M. J., Marra, P. P. and Daszak, P. 2006. West Nile virus epidemics in North America are driven by shifts in mosquito feeding behavior. – PLoS Biol. 4: e82.
Kimber, C. T. 1988. Martinique revisited. The changing plant geographies of a West Indian island. – Texas A & M Univ. Press.
Latta, S. C. and Ricklefs, R. E. 2010. Prevalence patterns of avian Haemosporida on Hispaniola. – J. Avian Biol. 41: 25–33.
Longmire, J. L., Maltbie, M. and Baker, R. J. 1997. Use of ''lysis buffer'' in DNA isolation and its implication for museum collections. – Occas. Pap. Mus. Texas Tech Univ. 163: 1–4.
Lovette, I. J., Bermingham, E., Seutin, G. and Ricklefs, R. E. 1998. Evolutionary differentiation in three endemic West Indian warblers. – Auk 115: 890–903.
Lovette, I. J., Bermingham, E. and Ricklefs, R. E. 1999. Mitochondrial DNA phylogeography and the conservation of endangered Lesser Antillean *Icterus* orioles. – Conserv. Biol. 15: 1088–1096.
Magurran, A. E. 1988. Ecological diversity and its measurement. – Princeton Univ. Press.
Martinsen, E. S., Perkins, S. L. and Schall, J. J. 2008. A three-genome phylogeny of malaria parasites (*Plasmodium* and closely related genera): evolution of life-history traits and host switches. – Mol. Phylogenet. Evol. 47: 261–273.
Matson, K. D. 2006. Are there differences in immune function between continental and insular birds? – Proc. R. Soc. B 273: 2267–2274.
Matson, K. D. and Beadell, J. S. 2010. Infection, immunity, and island adaptation in birds. – In: Morand, S. and Krasnov, B. R. (eds), The biogeography of host–parasite interactions. Oxford Univ. Press, pp. 217–232.
Nayar, J. K., Knight, J. W. and Telford, S. R. J. 1998. Vector ability of mosquitoes for isolates of *Plasmodium elongatum* from raptors in Florida. – J. Parasitol. 84: 542–546.
Outlaw, D. C. and Ricklefs, R. E. 2010. Comparative gene evolution in haemosporidian (Apicomplexa) parasites of birds and mammals. – Mol. Biol. Evol. 27: 537–542.
Perkins, S. L. and Schall, J. J. 2002. A molecular phylogeny of malarial parasites recovered from cytochrome b gene sequences. – J. Parasitol. 88: 972–978.
Ricklefs, R. E. and Lovette, I. J. 1999. The roles of island area per se and habitat diversity in the species–area relationships of four Lesser Antillean faunal groups. – J. Anim. Ecol. 68: 1142–1160.
Ricklefs, R. E. and Bermingham, E. 2001. Nonequilibrium diversity dynamics of the Lesser Antillean avifauna. – Science 294: 1522–1524.
Ricklefs, R. E. and Fallon, S. M. 2002. Diversification and host switching in avian malaria parasites. – Proc. R. Soc. B 269: 885–892.
Ricklefs, R. E. and Bermingham, E. 2004. History and the species–area relationship in Lesser Antillean birds. – Am. Nat. 163: 227–239.
Ricklefs, R. E. and Bermingham, E. 2008. The West Indies as a laboratory of ecology and evolution. – Phil. Trans. R. Soc. B 363: 2393–2413.
Ricklefs, R. E., Swanson, B. L., Fallon, S. M., Martinez-Abrain, A., Scheuerlein, A., Gray, J. and Latta, S. C. 2005. Community relationships of avian malaria parasites in southern Missouri. – Ecol. Monogr. 75: 543–559.
Scheuerlein, A. and Ricklefs, R. E. 2004. Prevalence of blood parasites in European passeriform birds. – Proc. R. Soc. B 271: 1363–1370.
Sokal, R. R. and Rohlf, F. J. 1995. Biometry. – W. H. Freeman.
Sol, D., Jovani, R. and Torres, J. 2000. Geographical variation in blood parasites in feral pigeons: the role of vectors. – Ecography 23: 307–314.
Stamatakis, A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. – Bioinformatics 22: 2688–2690.
Stamatakis, A., Hoover, P. and Rougemont, J. 2008. A rapid bootstrap algorithm for the RAxML web-servers. – Syst. Biol. 75: 758–771.
Super, P. E. and van Riper, C. III. 1995. A comparison of avian hematozoan epizootiology in two California coastal scrub communities. – J. Wildl. Dis. 31: 447–461.

Svensson, L. M. E. and Ricklefs, R. E. 2009. Low diversity and high intra-island variation in prevalence of avian *Haemoproteus* parasites on Barbados, Lesser Antilles. – Parasitology 6: 1121–1131.
Svensson-Coelho, M. and Ricklefs, R. E. 2011. Host phylogeography and beta diversity in avian haemosporidian (Plasmodiidae) assemblages of the Lesser Antilles. – J. Anim. Ecol. 80: 938–946.
Valkiunas, G. 2005. Avian malaria parasites and other haemosporidia. – CRC Press.
van Riper, C., III, van Riper, S. G., Goff, M. L. and Laird, M. 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. – Ecol. Monogr. 56: 327–344.
Weir, J. T. and Schluter, D. 2008. Calibrating the avian molecular clock. – Mol. Ecol. 17: 2321–2328.

Appendix 1. Prevalence of identified lineages of parasites recovered from each host species on each island. I = infected individuals, U = uninfected individuals, T = total individuals,% = haemosporidian prevalence (%).

	St Lucia				St Vincent				Grenada			
Host	I	U	T	%	I	U	T	%	I	U	T	%
Crotophaga ani (CAN)					0	3	3	0	0	1	1	0
Catheropeza bishopi (CBS)					0	5	5	0				
Coereba flaveola (CFA)	25	36	61	41	41	61	102	40.2	33	174	207	15.9
Coccyzus minor (CMI)									0	2	2	0
Columbina passerina (CPA)					5	11	16	31.3	3	9	12	25
Contopus latirostris (CLA)	0	5	5	0								
Cinclocerthia ruficauda (CRU)					0	1	1	0				
Dendroica adelaidae (DAD)	3	16	19	15.8								
Dumetella carolinensis (DCA)									0	1	1	0
Elaenia flavogaster (EFL)					0	10	10	0	5	18	23	21.7
Eulampis holosericeus (EHO)	0	3	3	0					0	11	11	0
Eulampis jugularis (EJU)	0	36	36	0	0	16	16	0				
Elaenia martinica (EMA)	6	35	41	14.6	0	9	9	0				
Glaucis hirsuta (GHI)									3	24	27	11.1
Geotrygon montana (GMO)	0	4	4	0	0	4	4	0	0	7	7	0
Icterus laudabilis (ILA)	0	5	5	0								
Loxigilla noctis (LNO)	46	25	71	64.8	22	25	47	46.8	1	42	43	2.3
Leptotila wellsi (LWE)									1	8	9	11.1
Molothrus bonairiensis (MBO)	0	2	2	0	0	1	1	0	0	4	4	0
Margarops fuscatus (MFT)	1		1	100								
Margarops fuscus (MFU)	12	8	20	60	0	9	9	0				
Myadestes genibarbis (MGE)	0	8	8	0								
Mimus gilvus (MGI)	2	3	5	40	0	4	4	0	3	13	16	18.8
Myiarchus nugator (MNU)					0	12	12	0	0	16	16	0
Myiarchus oberi (MOB)	0	1	1	0								
Melanospiza richardsoni (MRI)	1	6	7	14.3								
Orthorhynchus cristatus (OCR)	0	3	3	0	0	25	25	0	0	37	37	0
Quiscalus lugubris (QLU)	0	4	4	0					0	11	11	0
Ramphocinclus brachyurus (RBR)	1	4	5	20								
Saltator albicollis (SAL)	0	31	31	0								
Troglodytes aedon (TAE)					0	10	10	0	1	12	13	7.7
Tiaris bicolor (TBI)	10	8	18	55.6	8	71	79	10.1	1	35	36	2.8
Tangara cucullata (TCU)					0	13	13	0	0	15	15	0
Tyrannus dominicensis (TDO)	0	1	1	0	1	2	3	33.3	2	6	8	25
Turdus fumigatus (TFU)					1	12	13	7.7	3	8	11	27.3
Turdus nudigenis (TNU)	0	11	11	0	0	10	10	0	3	40	43	7
Vireo altiloquus (VAL)	11	45	56	19.6	9	9	18	50	1	6	7	14.3
Volatinia jacarina (VJA)									0	8	8	0
Zenaida auriculata (ZAR)									3	1	4	75
Zenaida aurita (ZAU)	0	1	1	0								
Grand total	118	301	419	28.2	87	323	411	21.2	63	509	572	11

Appendix 2. Details of the distributions of parasite lineages recovered on the islands of St Lucia, St Vincent and Grenada.

Lineage	Fallon et al. (2005)	SL	SV	GR	Total	Comments (see footnotes for location and sample abbreviations)
GA01	CPA1	0	2	2	4	There are no common ground doves in the SL sample; otherwise 88 samples broadly distributed in LA and GA, VZ, MEX; GQ141567 from *Columbina passerina* (Outlaw and Ricklefs 2010)
GA02	CPA2	0	3	1	4	There are no common ground doves in the SL sample; 43 samples primarily from GA and MEX; no sequence in GenBank
GD03	.	0	1	3	4	Otherwise, only TOL (from C), RSHA (CRC), and HAWA (HEX) this is almost identical to OZ05 (mostly vireos); no sequences in GenBank closer than 96% similarity
GD04	.	0	0	3	3	Unique to Grenada
JA4	**.**	**3**	**0**	**0**	3	All samples from EMA on SL, 4 recovered from TR/VE (EFL, QLU, TAE), 7 from JA (MPO, TCA, LVI, ECA, ILE, HVE), MEX = 1 (MGI); matches DQ659549 of Beadell et al. (2006) from *Geothlypis trichas*, and is 1 bp different from *P. elongatum* (AF069611) of Escalante et al. (1998)
LA01	HF	3	0	0	3	Total 66 samples, all mimids (MFU, MFT, CRU, CLH = 1) from LA and VE (3 MGI) and CT (DCA = 6); AF465572 from *Margarops fuscus* (Ricklefs and Fallon 2002: *Haemoproteus* haplotype 20)
LA02	HG	8	0	0	8	Total 17 LA mimids (MFT, MFU) including 2 MGI (VE) and 1 BCPT (DR); no closer than 94% sequence similarity to anything in GenBank
LA07	HD	2	6	38	59	Total 99 samples PR through LA, mostly CFA and most abundant in PR; same as DR03 (HJ of Fallon et al. 2005) (6 SV+19 CFA and LVI from DR); GQ141568 from *Coereba flaveola* (Outlaw and Ricklefs 2010)
LA08	HE	6	0	0	6	Total 23 LA (LNO) except TBI = 1 and VAL = 1; AF465569, Ricklefs and Fallon (2002), haplotype *Haemoproteus* 8, *L. noctis*; AY167245 (short sequence) (Fallon et al. 2003a), *L. noctis*. This lineage was not present in the 2000 sample from St Lucia (Fallon et al. 2004); not present in VE, TR, CC
LA19	HU3	1	0	0	1	Total 4 MFU, MO = 2, DO = 1, SL = 1; GQ141579 (Outlaw and Ricklefs 2010), *Margarops fuscus*
NA15	.	0	1	0	1	Also recovered from 1TFU (SV) and 1TMI (BRC)
OZ01	**PA**	**3**	**0**	**3**	6	Total 84 samples, varied hosts PR, J, BH (not DR) through LA and TR = 1 AIC; widespread in NA, MEX; AF465556, Ricklefs and Fallon (2002), *Passerina cyanea*, *Plasmodium* lineage 56; also many other sequences in GenBank
OZ02	HH	0	0	5	5	Total 203 samples; varied species, DR, PR, C (not J), MEX, QR, a few NA; GD are GHI, TAE, MGI, TNU = 2; AF465583, *Haemoproteus* lineage 35 of Ricklefs and Fallon (2002), *Piranga olivacea*
OZ04	**PC**	**29**	**0**	**4**	33	Total 196 samples; widespread, but particularly J and LA, TR = 3; Outlaw and Ricklefs (2010), GQ141587, *Coereba flaveola*; GQ141577, *Cinclocerthia ruficauda*
OZ08	**.**	**1**	**0**	**0**	**1**	Total 36 samples; various species OZ, M, and MEX; no other GA or LA
OZ10	HB	0	5	0	5	Total 28 samples, all OZ VOL; AF465576, haplotype *Haemoproteus* lineage 28, *Vireo olivaceus* (Ricklefs and Fallon 2002)
OZ12	.	2	2	0	4	Total 26 samples, mostly OZ VOL and LA VAL, plus 3 CC-VOL; AY817748 from OZ VOL; close to OZ10
OZ17	HA	3	0	0	3	Total 21 samples; 3 others LA, 8 CC-VOL, others PR, OZ VOL, VAL; AF465575, *Haemoproteus* lineage 27 from *Vireo altiloquus* (Ricklefs and Fallon 2002)
OZ21	HC	49	62	1	112	Total 294 samples; LA north to PR, common in CFA, LNO, LPO; unique on BA; AF465579, *Haemoproteus* lineage 31, *Loxigilla noctis* (Ricklefs and Fallon 2002); GQ141592, *Loxigilla portoricensis* (Outlaw and Ricklefs 2010)

Appendix 2 (*Continued*)

Lineage	Fallon et al. (2005)	SL	SV	GR	Total	Comments (see footnotes for location and sample abbreviations)
OZ36	**PB**	**3**	**0**	**0**	3	Total 8 samples; OZ-VOL =1, 4 MEX (VMA =2, VGR =2); OZ-VOL =1, 4 MEX (VMA =2, VGR =2). About 2% divergence from AY733089 *Plasmodium relictum* from *Zenaida macroura* (Beadell and Fleischer 2005)
OZ38	.	0	2	0	2	Total 5 (OZ =1, TR =2, PR =1)
Unique	.	5	3	3	11	
Total		118	87	63	268	

Locations: BA (Barbados), BH (Bahamas), BRC (Bird Rehabilitation Center, St Louis), C (Grand Cayman Island), CC (Cachacachare Island, Trinidad), CRC (Carolina Raptor Center), DO (Dominica), DR (Dominican Republic), GA (Greater Antilles), GD (Grenada), GR (Grenada), JA (Jamaica), LA (Lesser Antilles), M (Mobile, Alabama), MEX (Yucatan Peninsula, Mexico), MO (Montserrat), NA (North America), OZ (Ozark Mountains, Missouri), PR (Puerto Rico), QR (Qintana Roo, Mexico), SL (St Lucia), SV (St Vincent), TR (Trinidad), VE (Venezuela), VZ (Venezuela).
Host species: AIC (*Agelaius icterocephalus*), BCPT (*Phaenicophilus palmarum*), CFA (*Coereba flaveola*), CLA (*Contopus latirostris*), CRU (*Cinclocerthia ruficauda*), DCA (*Dumatella carolinensis*), ECA (*Eunornis campestris*), EFL (*Elaenia flavogaster*), EMA (*Elaenia martinica*), GHI (*Glaucis hirsuta*), HVE (*Helmithoros vermivorus*), ILE (*Icterus leucopteryx*), LNO (*Loxigilla noctis*), LPO (*Loxigilla portoricensis*), LVI (*Loxigilla violacea*), MAWA (*Dendroica magnolia*), MFT (*Margarops fuscatus*), MFU (*Margarops fuscus*), MGI (*Mimus gilvus*), MPO (*Mimus polyglottis*), QLU (*Quiscalus lugubris*), RSHA (*Buteo lineatus*), TAE (*Troglodytes aedon*), TBI (*Tiaris bicolor*), TCA (*Tyrannus caudifasciatus*), TFU (*Turdus fumigatus*), TMI (*Turdus migratorius*), TNU (*Turdus nudigenis*), VAL (*Vireo altiloquus*), VGR (*Vireo griseus*), VMA (*Vireo magister*), VOL (*Vireo olivaceus*).