The assembly of an island fauna by natural invasion: Sources and temporal patterns in the avian colonization of Barbados

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Abstract

By virtue of their isolation and depauperate faunas, oceanic islands offer unique opportunities to characterize the historical development of ecological communities derived from both natural and anthropogenic invasions. Barbados, an outlying island in the Lesser Antilles, was formed approximately 700,000 YBP by tectonic uplift and was then colonized by birds via natural invasion from the much older volcanic islands in the main Lesser Antillean arc. We investigated the timing and sources of the avian invasion of Barbados by determining levels of mitochondrial DNA (mtDNA) divergence between populations of eight bird species from Barbados and those on the nearby putative source islands of St. Lucia and St. Vincent. Although all Barbados populations appeared to be young relative to the geological age of the island, we found differences among species in their inferred times of colonization and we identified at least two sources of immigrants to Barbados. In contrast to these historical differences across species and populations, our characterization of the mitochondrial genotypes of 231 individual birds suggests that each island population represents the descendants of a single founding maternal lineage. Considered in concert, the results of this molecular survey indicate that the Barbados bird community is composed of species with different invasion histories, which in turn suggests that the island's community composition has changed repeatedly over its 700,000 year history.

Introduction

The timing, pattern, and origin of invasions across multiple species and communities are central themes in invasion ecology (e.g., Pimm 1989; Drake et al. 1993; Williamson 1994; Geller 1996; Vermeij 1996; Lockwood et al. 1997; Shigesada and Kawasaki 1997). The intrinsically historical nature of these processes reflects the fact that biological invasions proceed along a spectrum of temporal scales that spans ecological and evolutionary time (Brown 1989; di Castri 1989; Vermeij 1996). Although invasion biologists often study on-going invasions of anthropogenic origin, past natural invasions have presumably been subject to many of the same processes as contemporary human-mediated invasions. Thus, historical perspectives on natural invasions may help elucidate some of the phenomena that underlie biological invasions generally (Vermeij 1996). For example, studies of the sequence of invasions of the naturally defaunated island of Krakatau

(see Thornton 1996) have provided a classic example of patterns of community assembly mediated by dispersal-based natural biological invasion.

One bridge between the short-term ecological and long-term evolutionary aspects of invasion biology is the study of the geographic and temporal structure of community-wide natural invasions. Although placing invasion ecology on an evolutionary footing is a challenging goal, a number of phylogeographic studies have demonstrated that general evolutionary patterns can be inferred from molecule-based comparisons across sympatric taxa (e.g., Bermingham and Avise 1986; Hedges et al. 1992; Avise 1992; Joseph et al. 1995; Brumfield and Capparella 1996; Bermingham and Martin 1998; Losos et al. 1998). Most of these studies have included a small proportion of the taxa that comprise complex local or regional species assemblages; however, the most tractable systems for molecule-based studies of natural invasions permit phylogenetic assays of most species comprising the community.

Here, we present a mitochondrial (mtDNA)-based study of the evolutionarily young and relatively depauperate avian community of Barbados in which we have surveyed the majority of resident passerine species. Isolated tropical islands like Barbados are especially well suited for the study of general patterns of natural invasion because they have unusually high invasibility (e.g., Loope and Mueller-Dombois 1989; Erlich 1989) promoting the establishment of invading taxa. Barbados is unusual among isolated oceanic islands in that its bird community lacks endemic species and is entirely derived from natural invasion. In contrast to the anthropogenic introductions of birds to such oceanic islands as Hawaii (Loope and Mueller-Dombois 1989; Lockwood et al. 1993) and Tahiti (Moulton 1993), the bird species that colonized Barbados presumably did so via long-distance, over-water dispersal prior to the advent of modern human habitat alteration on the island. Barbados thus presents a unique opportunity to characterize the temporal and spatial structure of natural biological invasion on an evolutionary scale.

The geologic history of Barbados suggests that all colonization of the island by terrestrial organisms must have occurred relatively recently. Barbados was formed by uplift along the Lesser Antillean forearc (Speed 1994) and is the youngest of the major Lesser Antillean islands. An upper limit of roughly 700,000 years on emergence of Barbados has been determined by dating a step-like series of fossil coral reefs that cap the island (Mesolella 1967; Mesolella et al. 1970; Bender et al.

1979). In contrast, most other Lesser Antillean islands are of volcanic origin and are 20–30 million years older than Barbados (Speed 1994). Barbados was probably colonized by birds from source populations on these nearby, older islands. Our studies of Caribbean bird phylogeography have identified probable source populations for the eight Barbados species investigated here (Seutin et al. 1994; Bermingham et al. 1996, unpublished results). Available evidence has thus permitted us to focus our present study on birds from Barbados and the nearby islands of St. Vincent and St. Lucia, and in one case on the more distant island of Trinidad (Figure 1).

The genetic information presented here allows us to investigate several historical processes in the context of the avian invasion of Barbados. First, we determine if the Barbados population of each species is genetically differentiated from nearby conspecific populations and, in turn, identify the putative source population in cases where we observe genetic differences. This comparison allows us to examine the
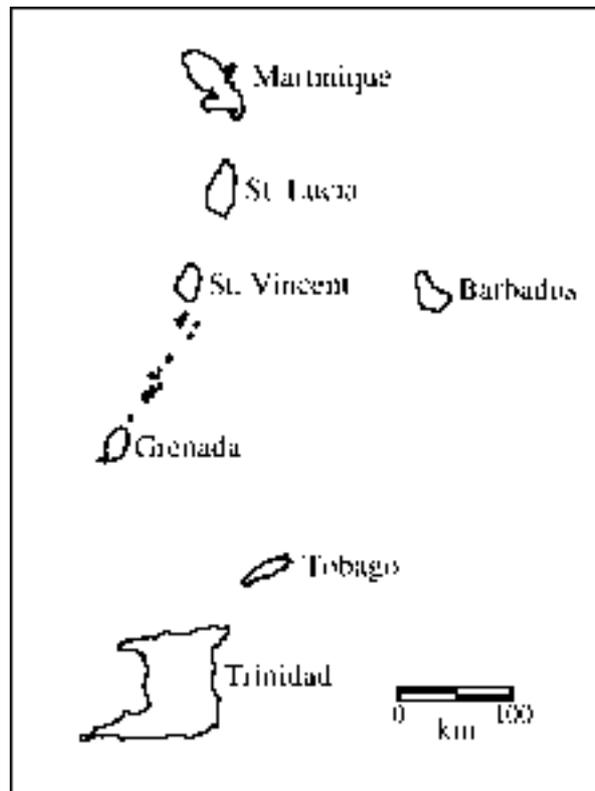

Figure 1. Map of the southern Lesser Antilles showing the location of Barbados relative to potential sources of avian immigrants.

spatial dynamics of invasion: was Barbados colonized as part of broader waves of invasion that spread across multiple islands, or did the avian invasion of Barbados proceed from long-established source populations? Second, we assess the frequency of immigration by surveying large numbers of Barbados individuals for the presence of paraphyletic lineages. The presence or absence of inter-island gene flow allows us to determine whether the populations that became established on Barbados have remained satellite constituents of geographically-widespread panmictic populations, or whether they have been historically independent following invasion of the island. Third, by assuming similar rates of mtDNA evolution across taxa, we compare the relative arrival time of each species to determine whether the eight species invaded Barbados simultaneously, as might be expected if they were responding in common to a single environmental change. In short, our molecular data allow us to determine whether the Barbados bird fauna is comprised of species with similar invasion histories or whether it represents a more ephemeral group of taxa with different sources and times of invasion.

Materials and methods

We employed a two-step approach to investigate mtDNA divergence and diversity. We first generated nucleotide sequence information for a small number of individuals representing each species and each island population to characterize general levels of inter-island differentiation. If these data produced evidence of geographically structured mitochondrial variation within a species, we then characterized all available samples (range 1 to 36 individuals/species/island; 232 individuals in total across the 8 species) either by additional mtDNA sequencing or by RFLP digestion of Polymerase Chain Reaction (PCR) mtDNA amplification products.

Samples were obtained by intensive mist-netting on Barbados (12–18 May 1993), St. Vincent (19–31 May 1993), and St. Lucia (18–26 July 1991). Pectoral muscle biopsies and blood samples were collected non-destructively (Seutin et al. 1993) and preserved as in Seutin et al. (1991). Additional tissue samples from St. Vincent were obtained from the National Museum of Natural History, Washington, DC (Table 1). All samples were collected and transported under the appropriate permits and licenses. Eight species (Table 1) were chosen for inclusion in this study based on the availability of tissue samples suitable for genetic analyses; samples from the remaining four resident Barbados landbirds could not be obtained either because the species is extinct (*Margarops fuscus*) or severely endangered (*Dendroica petechia*) on Barbados, or because individuals were not captured in our mist-nets (*Sericotes holosericeus* and *Tyrannus dominicensis*).

DNA extractions followed the protocol of Seutin et al. (1993). We amplified a 1074 bp segment of mtDNA that spanned the full tRNA[Lys], ATPase 8, and ATPase 6 genes through the PCR with the primer pair CO2GQL and CO3HMH (primer sequences and amplification conditions are available upon request from E. Bermingham). Amplification products were cut from LMPA gels following electrophoresis, purified using the Geneclean© procedure, and sequenced

Table 1. Mitochondrial differentiation among island populations of eight Lesser Antillean birds. Sample size indicates number of individuals for which the entire ATPase 6 and ATPase 8 nucleotide sequences were determined (at left) and the total number of individuals characterized by either RFLP assays or DNA sequencing (at right). MtDNA divergence values indicate the uncorrected pairwise nucleotide difference between the most similar individuals from each pair of islands. Islands from which samples were obtained abbreviated: (BA) Barbados, (SL) St. Lucia, and (SV) St. Vincent, except for the common ground dove where the northern Lesser Antilles were represented by two samples from Martinique rather than St. Lucia. NMNH accession numbers of St. Vincent samples are: elaenia 2115 and 2116; bananaquit 2909 and 2141; bullfinch 2086 and 2111; grassquit 2132 and 2164; grackle 2125.

Species	Number of individuals examined			Minimum % nucleotide divergence		
	SV	BA	SL	SV-BA	SL-BA	SV-SL
Common ground dove (*Columbina passerina*)	2/2	2/2	2/2	0.12	0.00	0.12
Black-faced grassquit (*Tiaris bicolor*)	2/2	2/2	2/2	0.12	0.00	0.00
Caribbean elaenia (*Elaenia martinica*)	2/8	2/12	2/21	0.36	0.24	0.36
Lesser Antillean bullfinch (*Loxigilla noctis*)	2/36	5/21	5/32	0.60	0.36	0.48
Black-whiskered vireo (*Vireo altiloquus*)	2/7	2/11	2/26	3.80	0.24	3.70
Bananaquit (*Coereba flaveola*)	11/11	9/9	9/9	0.83	0.24	0.83
Antillean crested hummingbird (*Orthorhyncus cristatus*)	2/2	1/1	2/2	1.07	1.19	0.12
Carib grackle (*Quiscalus lugubris*)	1/1	2/9	2/2	3.44	3.44	0.12

in the L direction using DyeDeoxy Terminator Cycle Sequencing (Applied Biosystems Division of Perkin Elmer, Inc.) with the primers CO2GQL, LYSL, PKL, PKLD, and TPL. The samples were then electrophoresed in an Applied Biosystems 373A DNA sequencer.

Estimates of inter-island nucleotide divergence were based on the overlapping coding region of the ATPase 6 and ATPase 8 genes. The minimum uncorrected percent pairwise divergences of nucleotide substitutions between allopatric individuals were used as measures of phylogenetic relationships between populations under the assumption that the accumulation of substitutions is approximately clock-like over the small inter-island genetic distances calculated here (e.g., Martin et al. 1992; Bermingham and Lessios 1993; Knowlton et al. 1993). Cladistic analyses supported the phylogeographic patterns suggested by genetic distance-based analyses (Lovette, personal observation); distance-based results alone are reported here as they provide additional information on the amount of sequence divergence between populations.

Our sequencing strategy was based on the assumption that the island populations surveyed are monophyletic with respect to conspecific populations on nearby islands. If this assumption is met, then samples from only a few individuals per population are required to reconstruct the relationships of those populations. Unfortunately, confirmation of monophyly requires very large sample sizes, especially when immigrant haplotypes are present at low frequencies (Avise 1994). To examine this assumption of single-island monophyly, we genetically 'typed' all available samples (Table 1) of five species via either RFLP digestion of PCR products or by additional DNA sequencing.

In order to identify island-specific RFLP markers, we searched our ATPase sequences for nucleotide sites that (1) varied between but not within conspecific populations, and (2) could be cleaved diagnostically by a commercially available restriction enzyme. Although the low nucleotide divergence between the haplotypes in many pairs of populations (see results) limited the number of potentially diagnostic nucleotide differences, we identified RFLP markers in the Caribbean elaenia (cut with enzyme *Tsp*509I), black-whiskered vireo (cut with enzyme *Ava*II), and Lesser Antillean bullfinch (cut with enzymes *Hae*III, *Ban*II, and *Bst*NI). Amplification products were obtained as described above and digested with 5–10 units of enzyme. Digestion products were electrophoresed on a 2.25% agarose gel and compared with restriction profiles predicted from sequence data; a typical RFLP gel is shown in Figure 2. The presence or absence of these diagnostic nucleotide differences and associated RFLP sites allowed us to assay the phylogenetic affinity of each sample: if all samples from a population shared an identical RFLP profile, then we concluded that the shared diagnostic nucleotide substitution indicated the monophyly of that population with respect to populations with different RFLP profiles. It should be noted that these RFLP assays represent biased samples of the mtDNA genome and thus do not provide additional information on levels of nucleotide diversity within populations or on the magnitude of differentiation among haplotypes or populations.

Results and discussion

An important goal of historical invasion biology is the elucidation of the ecological and evolutionary patterns that underlie the assembly of invasion-derived communities (Vermeij 1996). The avian invasion of Barbados provides a unique opportunity to characterize the sources, timing, and frequency of the natural avian invasion on an isolated oceanic island. We sequenced the full 842 bp of the overlapping ATPase 6 and ATPase 8 genes for 75 individuals of eight species (Table 1). No length variation was noted and sequence alignments were in all cases unambiguous. All unique haplotypes have been deposited in GenBank (accession numbers AF132365–AF132439 inclusive). Our results suggest that the Barbados avifauna is composed of species with different invasion histories, and we have divided the eight species into four qualitative groups (Figure 3) based on the geographic structure of their mtDNA variation.

Group I: low nucleotide diversity and geographic structure

Two species, the grassquit (*Tiaris bicolor*) and the dove (*Columbina passerina*), were genetically panmictic in the sense that they showed little or no geographically structured mitochondrial variation between the three islands (Table 1). Pairs of grassquits on Barbados/St. Lucia and St. Lucia/St. Vincent shared identical haplotypes (Table 1). mtDNA variation in the dove was similarly low, as the four individuals from Barbados and Martinique had identical ATPase haplotypes. The two St. Vincent doves differed from
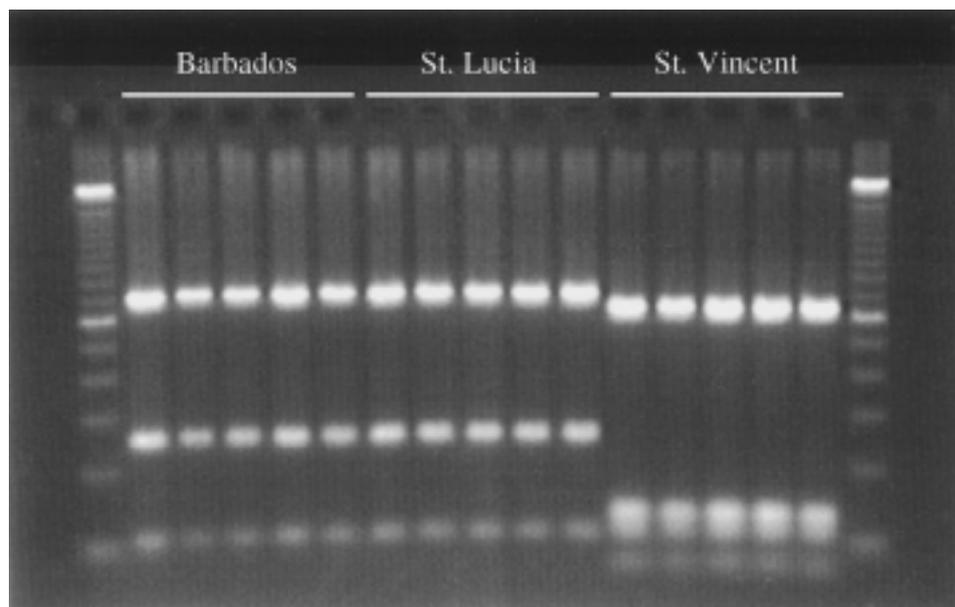
Figure 2. Representative RFLP gel illustrating island-specific mitochondrial haplotypes of Lesser Antillean bullfinches (*Loxigilla noctis*) from Barbados, St. Lucia, and St. Vincent (five individuals/island shown here). Fragment profiles were generated by digestion of ATPase PCR fragment with restriction enzyme *Hae*III, which distinguished all St. Vincent bullfinches from conspecifics found on Barbados and St. Lucia. The use of additional restriction enzymes (not shown) permitted us to distinguish Barbados and St. Lucia individuals. Outermost gel lanes represent a 100 bp 'ladder' DNA size standard.

one another at two nucleotide sites and from the Martinique/Barbados haplotype by one to three substitutions. Although doves from the intermediate island of St. Lucia were not sampled, they presumably also belong to this panmictic group. The low island-specific nucleotide divergences in the grassquit and dove suggests that these species have either maintained high levels of gene flow across the southern Lesser Antilles or that they have each recently invaded at least two of the three islands we surveyed.

Group II: moderate nucleotide diversity with equivalent pairwise distances among the three islands

The elaenia (*Elaenia martinica*) and bullfinch (*Loxigilla noctis*) had somewhat greater levels of nucleotide diversity and exhibited modest levels of geographically structured genetic variation. In these species, minimum pairwise divergences were roughly equal among all three islands: elaenias from different populations were distinguished by two to three substitutions, whereas bullfinches had accumulated three to five substitutions among islands (Table 1). In both species, our RFLP-based survey of large numbers of

individuals found no evidence of paraphyly within any population. This absence of multiple invasions coupled with the presence of population-specific mtDNA haplotypes indicates that gene flow among islands has not been frequent enough to override mtDNA differentiation between the island populations. As the St. Lucia–St. Vincent divergences are roughly equal to the Barbados-specific divergences in these taxa, a parsimonious explanation for their regional pattern of mitochondrial variation is that the ancestral mtDNA lineages representing both species invaded the southern Lesser Antilles in single waves after the emergence of Barbados.

Group III: high nucleotide diversity and strong geographic structure

Although we observed island-specific sequence divergence in the vireo (*Vireo altiloquus*) and bananaquit (*Coereba flaveola*), the magnitude of divergence in these species was not equivalent across all pairs of islands. Whereas the vireo and bananaquit had St. Lucia–Barbados divergence values similar to those of the elaenia and bullfinch, the vireo and bananaquit had much larger divergences (Table 1) between their
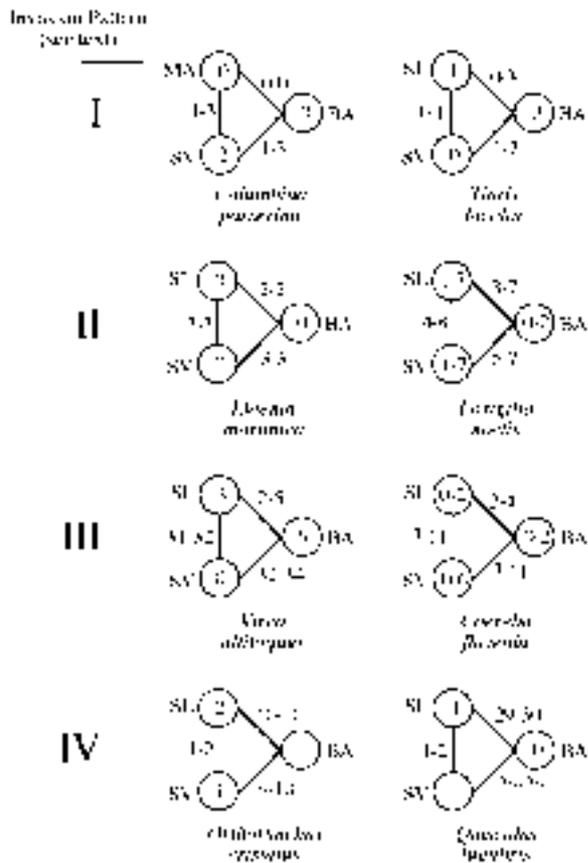
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Figure 3. Range of pairwise nucleotide differences within (inside circles) and between (along branches) island populations of eight Lesser Antillean birds. See Table 1 for island abbreviations and sample sizes.

St. Vincent–Barbados and St. Lucia–St. Vincent populations. Our genetic characterization of larger numbers of vireos and bananaquits from the three islands (Table 1) found evidence of only monophyletic lineage**s** on each island. Additional published (Seutin et al. 1994) and unpublished results (Bermingham and Ricklefs, personal communication) representing vireos and bananaquits from the majority of Lesser Antillean islands permit the strong inference that the St. Lucia and St. Vincent vireo and bananaquit populations diverged during a long period of residency on these islands, followed by comparatively recent invasion of Barbados from St. Lucia.

Group IV: high Barbados-specific mtDNA differentiation

The Barbados populations of the hummingbird (*Orthorhyncus cristatus*) and grackle (*Quiscalus*

lugubris) showed considerable sequence divergence from their St. Lucia and St. Vincent conspecifics, whereas genetic distances between St. Lucia and St. Vincent populations were negligible (Table 1). A regional survey of Caribbean grackles from their entire Antillean range and several continental locations identified Trinidad as the probable source of the Barbados grackle population (Bermingham and Ricklefs, unpublished results): this comparison of the ATPase coding region of 11 Trinidadian grackles with the two Barbados individuals revealed that the Barbados grackles share identical haplotypes with some Trinidadian individuals. All other natural Lesser Antillean grackle populations differ from the Barbados individuals by more than 3% ATPase divergence. The Barbados population of the Antillean crested hummingbird may have similarly invaded Barbados from an island other than St. Lucia or St. Vincent, but confirmation of this possibility requires a more complete phylogeographic survey.

Historical patterns in the avian invasion of Barbados

As described above, our molecular survey documented differences among bird species in the sources and timing of invasion (Figure 3). Six of the eight Barbados populations were genetically differentiated from conspecific populations on the nearby islands of St. Vincent and St. Lucia. Based on genetic affinities, we identified St. Lucia as the probable source of invasion for three of these six differentiated populations, whereas two species seem to have colonized Barbados from outside of our study area. Under the assumption of roughly clock-like accumulation of mitochondrial substitutions, the across-species differences in the magnitude of Barbados-specific genetic differentiation suggest a concomitant heterogeneity of invasion time. These findings support the hypothesis that dispersal-derived communities with access to multiple invasion sources will be composed of species with different invasion histories.

In contrast to this apparent heterogeneity in invasion source and timing, we found evidence of only a single founding lineage within each island population. Surveying populations for the presence of multiple lineages is difficult, as the probability of not detecting rare lineages is high when only a few individuals are examined (Avise 1994). However, when we genetically characterized 7 to 36 individuals/population of four differentiated species (Table 1) we found no evidence of paraphyly within any single population: in all cases,

individuals from a given island were more similar to each other than they were to any individual from a different island. This general pattern of low lineage diversity within Barbadian bird populations indicates that between-island gene flow has been rare relative to the processes of lineage sorting and mitochondrial divergence. Although we can not completely discount the possibilities of multiple invasions of Barbados from different sources or of repeated invasions masked by the complete replacement of resident mtDNA lineages, the available evidence suggests that successful immigration is infrequent, even on an evolutionary time scale.

Our interpretations of the phylogenetic patterns described above are based on the assumption that among-species differences in Barbados-specific mitochondrial divergence stem from differences in the species' respective times of initial invasion. We recognize, however, that small among-species differences in Barbados-specific divergence may not be statistically resolvable. In contrast, the differences between the St. Lucia and St. Vincent populations of the vireo and bananaquit are clearly larger (Table 1). In all cases, increased nucleotide sampling would allow a more refined analysis of invasion time under the assumption of a molecular clock.

Comparisons of mtDNA divergence levels with geological information on Barbados suggest that the Barbados bird populations are young relative to the age of the island. Studies of recently separated species with 'known' histories (Martin et al. 1992; Bermingham and Lessios 1993; Knowlton et al. 1993) have suggested an approximately clock-like accumulation of mtDNA substitutions, and mitochondrial variation is commonly assumed to accumulate in birds at a rate of approximately 2%/million years (Shields and Wilson 1987; Randi 1996; Nunn et al. 1996; Tarr and Fleischer 1993; Klicka and Zink 1997; Fleischer et al. 1998). Assuming this rate of divergence, birds that colonized Barbados soon after the island's emergence at 0.7 million years ago should have accumulated 1.4% sequence divergence. In contrast, the most genetically divergent Barbados population clearly allied to neighboring populations is only 0.36% distinct (Table 1). It is unlikely that errors in dating the age of the island are responsible for this discrepancy, as the evidence for a continuously emergent island surface for at least the past 640,000 years is strong (Bender et al. 1979).

A likely explanation for the consistently low Barbados-specific levels of mitochondrial divergence is that the Barbados bird populations are considerably younger than the island they inhabit. Previous studies of naturally defaunated islands have demonstrated that colonization by birds may occur rapidly once suitable habitat becomes available (e.g., Thornton et al. 1990; Zann et al. 1990). In contrast, our results suggest that the founders of the avian mtDNA lineages now present on Barbados arrived on the island long after its emergence. Other species, or different mtDNA lineages of the species now found on Barbados, may have been present on the island earlier and since become extinct, but our methods of molecular inference allow us to examine only those populations that have survived to be sampled. If this time lag scenario is correct, 'suitable' habitat may have been available on Barbados long before the current bird species invaded the island. Similar invasion lags over shorter time scales are a frequent and often inexplicable feature of contemporary invasions (Carlton 1996; Shigesada and Kawasaki 1997). As the genetic evidence suggests that at least some of the avian taxa now found on Barbados (group III; Figure 3) were present on nearby Lesser Antillean islands long before Barbados was colonized, whereas other species (groups I and II) may have moved through the islands in contemporaneous waves of invasion, the factors responsible for these disparate historical invasion patterns are likely to be species-specific.

In summary, although the Barbados bird community as a whole appears to be recently derived relative to the age of the island, the species now found on Barbados invaded the island from at least two different sources. Ongoing inter-island gene flow appears to be rare. The heterogeneity in invasion source and timing of the Barbados avifauna demonstrates that historical congruence may be unusual in dispersal-derived communities and suggests that the composition of even simple bird communities may vary over short evolutionary periods due to the different invasion histories of their constituent taxa.

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