# HISTORICAL BIOGEOGRAPHY OF THE BANANAQUIT (*COEREBA FLAVEOLA*) IN THE CARIBBEAN REGION: A MITOCHONDRIAL DNA ASSESSMENT

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*Abstract.*—We analyzed mitochondrial DNA (mtDNA) restriction-site variation in bananaquit (*Coereba flaveola*; Aves, Coerebinae) populations sampled on 12 Caribbean islands and at 5 continental localities in Central America and northern South America. Multiple fixed restriction-site differences genetically defined several regional bananaquit populations. An mtDNA clade representing all Jamaican bananaquits was the most divergent; the estimated average sequence divergence ($d_{xy}$) between Jamaican and all other mtDNA haplotypes surveyed was 0.027. Three groups of populations, representing Central America, northern South America, and the eastern Antilles (Puerto Rico to Grenada) were nearly equally differentiated among themselves (average $d_{xy}$ = 0.014), and may represent a single, recent range expansion. Within the eastern Antilles, three geographically restricted haplotype groups were identified: Puerto Rico, north-central Lesser Antilles (U.S. Virgin Islands to St. Lucia), and Grenada–St. Vincent. The evolutionary relationships of these groups were not clear. Genetic homogeneity of the island populations from the U.S. Virgin Islands to St. Lucia suggested a recent spread of a specific north-central Lesser Antillean haplotype through most of those islands. Haplotype variation across this region indicated that this spread may have occurred in two waves, first through the southernmost islands of St. Lucia, Martinique, and Dominica, and more recently from Guadeloupe to the north. The geographic distribution of mtDNA haplotypes, and of bananaquit populations, suggests periods of invasiveness followed by relative geographic quiescence. Although most genetic studies of bird populations have revealed homogeneity over large geographic areas, our findings provide a remarkable counterexample of strong geographic structuring of mtDNA variation over relatively small distances. Furthermore, although the mtDNA data were consistent with several subspecific distinctions, it was clear that named subspecies do not define equally differentiated evolutionary entities.

*Key words.*—Bird, Caribbean region, *Coereba flaveola*, genetic divergence, genetic diversity, historical biogeography, mtDNA, RFLP, West Indies.

Received June 15, 1993. Accepted September 15, 1993.

Historical biogeography is concerned with reconstructing the history of geographic distributions of populations and species. Such reconstructions help us to understand the dynamics of evolutionary changes in species and of ecological changes in communities. Contemporary distributions and inferences about genetic divergence obtained from phenotypic characters provide the basis for most biogeographic analyses at the taxonomic level of the species (Brooks and Mc-Lennan 1991). DNA restriction-site analysis and DNA sequencing now provide important data for historical biogeography because they permit direct measurement of genetic divergence between populations or genotypes and increased certainty in the inference of the history of genetic changes (Bermingham and Avise 1986; Avise et al. 1987; Avise 1992; Bermingham et al. 1992). In addition, application of the molecular-clock concept permits a rough dating of divergence times, which may then be compared to histories of climate change and the dates of geologic events having biogeographic consequence.

Although most terrestrial species are distributed on continental land masses, archipelagoes provide excellent opportunities for historical biogeographic analyses. For biogeographers, the primary advantage of island groups over continents lies in the subdivision of species into discrete, geographically isolated populations. Thus, distributions can be defined in terms of presence or absence on an island-by-island basis, and phenotypic or genotypic variation can be characterized by within-population and between-population variance components that clearly match discrete populations. The analysis of genetic variation within and among island populations

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provides a powerful tool for assessing the historical development of biogeographic patterns and the processes responsible for these patterns (Rosen 1976, 1978; Kluge 1988).

One island chain that has been the focus of much attention from biogeographers, and which is central to the present study, is the Lesser Antilles. The geologic and biogeographic histories of those Caribbean islands have been summarized in several recent studies (Pregill 1981; Sykes et al. 1982; Rosen 1985; Roughgarden 1990). The island arc that forms the present-day Lesser Antilles is believed to have cleared the southeastern edge of the Bahama Platform on its eastward movement across what is now the Caribbean Basin approximately 35 mya (Burke 1988). The formation and present-day positioning of the Lesser Antilles are undoubtedly more recent, that is, 20+ mya, but certainly antedate the appearance of the study species, the bananaquit *Coereba flaveola*, in the archipelago. Lowered sea levels during the glacial maxima of the Pleistocene did not substantially alter the area and isolation of most Lesser Antillean islands, although larger banks exposed during glacial maxima provided terrestrial connections between some islands (e.g., Puerto Rico and some of the Virgin Islands; St. Kitts and Nevis; Antigua and Barbuda) (Donnelly 1988).

Knowledge about biogeographic and evolutionary processes allows the generation of historical biogeographic premises. First, space and history should be generally related; one expects individuals or genotypes that are genetically more divergent to be geographically more distant. Second, genetic divergence increases with time and with the strength of barriers to dispersal between populations. Third, when one population is a genetic subset of another population, the latter is likely to be ancestral, assuming that the two populations had similar demographic histories. These premises may be used to interpret the historical development of biogeographic patterns. For example, if genetic relationships over island chain A-B-C were 1-3-2, a more complex history of colonization than a simple island-by-island stepping-stone model could be inferred. In this particular case, island B would have been colonized last from island C, indicating either haphazard dispersal or recolonization following extinction of the population on B. If the distribution of genotypes was 1-1-1 over the same island group, probably either colonization was recent and also rapid compared to genetic change, or

individuals migrate readily between islands, forming a single, genetically homogenous population.

We previously used those biogeographic premises to interpret the history of the streaked saltator (*Saltator albicollis;* Seutin et al. 1993) and of the yellow warbler (*Dendroica petechia;* Klein 1992) in the Caribbean. Populations of the streaked saltator on the adjacent islands of Dominica, Martinique, and St. Lucia in the Lesser Antilles share most mitochondrial DNA (mtDNA) restriction-site haplotypes and exhibit a maximum genetic divergence among haplotypes ($d_{xy}$) of 0.006. Recent derivation of the populations from a common ancestor, rather than a high level of migration between islands, is indicated by the limited Caribbean distribution of the species to the central part of the Lesser Antilles. High migration levels would probably further colonization of the island chain. Antillean haplotypes differ from continental haplotypes of the same species by $d_{xy}$ values exceeding 0.06, further implying low vagility. On some of the islands occupied by saltators, Klein (1992) observed two coexisting mtDNA haplotypes in the yellow warbler that differed by $d_{xy} = 0.0135$, one of West Indian origin and the other of Venezuelan derivation. This suggests a more complex origin for Lesser Antillean populations of the yellow warbler, compared to those of the streaked saltator, with invasion from two genetically differentiated source areas.

Here we continue an appraisal of historical biogeography and evolution of Antillean landbirds by reporting on levels of intrapopulation variability and interpopulation differentiation in mtDNA among island populations of *C. flaveola*. The bananaquit is a small (8–12 g; Faaborg and Winters 1979), nectarivorous and frugivorous emberizine (Passeriformes) of uncertain affinities. In recent treatments, it has been variously placed in a monotypic subfamily (Coerebinae; e.g., American Ornithologists' Union 1983) or with the tanagers (Thraupini; e.g., Sibley and Monroe 1990). It is widely distributed, mainly in lowland habitats, from southern Mexico, through Central America and the West Indies, to most of humid-tropical South America (fig. 1). Its abundance varies greatly through its range; it is most numerous in semiopen to open habitats and is scarce or even absent from extensively forested regions, particularly in continental areas. The bananaquit is especially common on islands and probably is the most abundant bird

species in the West Indies (Lack 1976, Cox and Ricklefs 1977, Wunderle 1985).

According to Bond (1963, p. 93), *C. flaveola* is of South American origin, and West Indian populations have resulted from two invasions: "one entering via Grenada and spreading north and west to Jamaica, the other from Central America, spreading north and east to the Bahamas." Thus, two subspecies groups are recognized in the West Indies (Bond 1956, 1963): the *bahamensis* group from the Bahamas (*bahamensis*), Cayman Islands (*sharpei*), coastal islands off Yucatan (*caboti*), Isla Providencia (*tricolor*) and Isla San Andres (*oblita*); and the Antillean group of 11 subspecies considered in this article (table 1). In total, Paynter (1968) recognized 41 bananaquit subspecies, based primarily on variation in plumage coloration. In addition to this geographic variation in plumage, the species exhibits plumage dimorphism on the islands of Grenada (subspecies *aterrima*), St. Vincent (*atrata*), Los Testigos (*laurae*), and Los Roques (*lowii*), where individuals with both normal and melanistic plumage occur. This polymorphism has been described in detail by Wunderle (1981a,b,c, 1983).

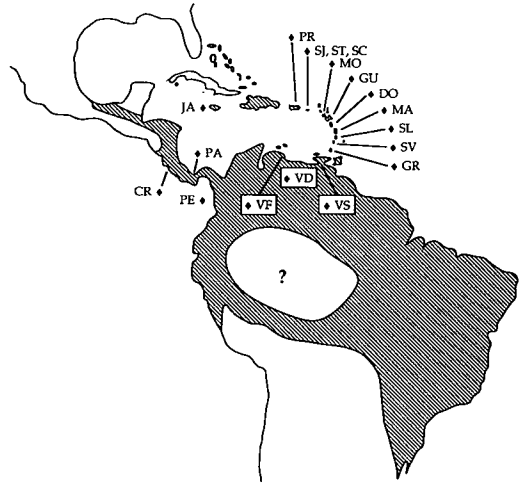Our genetic analysis of *C. flaveola* in the Caribbean region thus considers a species with highly variable phenotypes having a widespread distribution which includes the Lesser Antilles, a chain of long-isolated, oceanic islands that could have been colonized only by overwater dispersal. This study offers insights on avian colonization of the West Indies that address the relationship between history and biogeographic patterns. Our results also provide additional evidence suggest-



FIG. 1. Geographic distribution of *Coereba flaveola* with collection localities indicated. Acronyms for localities are defined in table 1.

TABLE 1. Subspecies and samples of the bananaquit from the West Indies and continental locations around the Caribbean Basin. ns, not sampled.

| Subspecies | Location | Code | Sample size | Haplotype diversity | Nucleotide diversity |
|---|---|---|---|---|---|
| *flaveola* | Jamaica | JA | 10 | 0.889 | 0.00369 |
| *bananivora* | Hispaniola | | ns | | |
| *nectarea* | Tortue | | ns | | |
| *portoricensis* | Puerto Rico | PR | 25 | 0.853 | 0.00213 |
| *sanctithomae* | St. Thomas | ST | 1 | | |
| | St. John | SJ | 1 | | |
| *newtoni* | St. Croix | SC | 10 | 0.378 | 0.00054 |
| *bartholemica* | Montserrat | MO | 5 | | |
| | Guadeloupe | GU | 6 | | |
| | Dominica | DO | 19 | 0.790 | 0.00274 |
| *martinicana* | Martinique | MA | 8 | | |
| | St. Lucia | SL | 18 | 0.758 | 0.00188 |
| *barbadensis* | Barbados | | ns | | |
| *atrata* | St. Vincent | SV | 15 | 0.848 | 0.00202 |
| *aterrima* | Grenada | GR | 17 | 0.544 | 0.00080 |
| *luteola* | Venezuela (Sucre) | VS | 12 | 0.758 | 0.00258 |
| | Venezuela (Distrito Federal) | VD | 4 | | |
| | Venezuela (Falcon) | VF | 2 | | |
| *mexicana* | Panama (Bocas del Toro) | PA | 8 | | |
| | Costa Rica | CR | 1 | | |
| *cerinoclunis* | Panama (Pearl Islands) | PE | 8 | | |
| | Total | | 170 | | |

ing that Neotropical bird species exhibit more phylogeographic structure than their temperate counterparts.

## MATERIALS AND METHODS

*Field Methods.*—We obtained 170 tissue samples of bananaquits from Jamaica, Puerto Rico, the three U.S. Virgin Islands, seven Lesser Antillean islands, three locations in Venezuela, the Pearl Islands off the Pacific coast of Panama, the province of Bocas del Toro on the Atlantic coast of Panama, and the Pacific coast of Costa Rica (table 1, fig. 1). Detailed information on sampling localities is available from the authors. Both light-phase and dark-phase color morphs were represented in our samples from Grenada and St. Vincent. Each sample consisted of tissues collected primarily from adult birds; judging from the presence or absence of a cloacal protuberance in the biopsied birds, or from gonadal inspection on collected specimens, both sexes were represented in most samples.

Three Puerto Rican specimens were obtained as whole corpses that had been stored at −20°C for up to several years; we extracted genomic DNA from the pectoral muscle of these specimens. Most samples from Dominica, Martinique, St. Lucia, Grenada, Venezuela, and the Pearl Islands consisted of pectoral muscle biopsies of mist-netted birds. The biopsy procedure followed Baker (1981), except that we excised a triangular piece of the lower part of the breast muscle; birds were released within an hour of the procedure. We preserved the samples at ambient temperature in the field in a salt-dimethyl sulfoxide (DMSO) solution (Seutin et al. 1991). All other tissue samples were collected from sacrificed birds, stored in the field in liquid nitrogen, and later transferred to ultracold (−70°C) freezers. All samples were collected and imported under appropriate permits and licenses. Voucher specimens for the bananaquits collected by Klein have been deposited in the following research collections: Museum of Zoology, University of Michigan; Department of Natural Resources, Puerto Rico; Field Museum of Natural History, Chicago; Fundación La Salle, Caracas, Venezuela.

*DNA Extraction, Restriction Digests, Electrophoresis, Southern Blotting, and Probing.*—We extracted total cellular DNA from most samples using the CTAB extraction procedure described in Seutin et al. (1993). We typically used pectoral muscle for these extractions; on occasion, however, liver, brain, kidney, heart, or lung tissues were also used. The DNAs were not dialyzed before restriction analysis, because we have found this step unnecessary. Purified mtDNA was obtained from 24 individuals from five sampling locales (Jamaica, Puerto Rico, Guadeloupe, Dominica, and Venezuela) by ultracentrifugation in cesium chloride-propidium iodide (CsCl-PI) density gradients, following the protocols of Dowling et al. (1990) and Klein (1992).

For the Southern blotting analyses, approximately 2 μg of total DNA or 1 ng of purified mtDNA was digested with 5–10 units of enzyme, following the manufacturer's recommendations. We used 2 enzymes with $r$ values equal to 5.3 (*Ava* I and *Hinc* II) and 14 enzymes with $r$ values equal to 6 (*Bam*H I, *Bgl* I, *Bgl* II, *Cla* I, *Dra* I, *Eco*R I, *Eco*R V, *Hin*d III, *Nco* I, *Nde* I, *Pst* I, *Pvu* II, *Sac* I, and *Stu* I). Restriction fragments were separated electrophoretically in 1.0% agarose gels and blotted by capillarity onto Zetabind® membrane as detailed in Seutin et al. (1993).

Two to four blots were prehybridized at once in canisters rotating at approximately 5 rpm. Prehybridizations were conducted at 65°C for 1–3 h, in 20–30 ml of solution (10% dextran sulfate, 0.5M NaCl, 1% SDS). We used a bananaquit mtDNA preparation purified two times on CsCl-EtdBr gradients as a probe. Traces of nuclear DNA were removed from this probe by running native or *Eco*R I-digested aliquots in 0.9% low-melting point agarose gels and extracting the mtDNA fragments with the GeneClean® procedure (Bio101, LaJolla, Calif.). In random priming reactions, a few nanograms of probe were radioactively labeled with [α-³²P]dCTP to very high specific activity ($10^8$–$10^9$ dpm/μg). Blots were hybridized for 12–18 h, and then washed as described by Seutin et al. (1991). Scorable bands on autoradiographs were obtained in 16–120 h on Kodak XAR® film at −70°C using one intensifying screen. No attempt was made to score fragments smaller than 300 base pairs (bp).

*Mapping.*—We physically mapped the position of most restriction sites in single individuals from Puerto Rico and Venezuela (haplotypes PR12 and VE7), using a double-digestion strategy (Dowling et al. 1990). Typically, 1–2 ng of purified mtDNA were digested simultaneously or sequentially with two enzymes, fragments were end-labeled with the appropriate [α-³²P]dNTP, and electrophoresed in polyacrylamide and agarose gels that were then dried and exposed to

autoradiographic films (for details, see Klein 1992). Mapped restriction sites (fig. 2) are presented relative to the single *Cla* I site found in the two clones; the homology of this site in the mapped haplotypes was verified by double digestion with *Sac* II (Brown 1985). The *Cla* I site is in the 12S rRNA gene, and in chickens is located 332 bp from the *Sac* II site (Desjardins and Morais 1990).

We did not map, in the Puerto Rican individual, one *Pvu* II and two *Hind* III sites, and in the Venezuelan individual, one *Ava* I and two *Hind* III sites, nor did we map the six *Nde* I restriction sites, or the 14 *Stu* I sites.

*Restriction-Site Data Analysis.* —Each distinctive mtDNA fragment pattern for a restriction enzyme was given an alphabetic label. The list of fragment sizes for each restriction pattern and the matrix of presence-absence of restriction sites for each haplotype are presented in appendixes 1 and 2, respectively. In three individuals, low DNA yield precluded identification of haplotypes for one or two enzymes (one individual from Dominica with *Hind* III, one from Martinique with *Hind* III and *EcoR* V, and one from St. Vincent with *EcoR* V). In each case, the most common haplotype for that enzyme in that population was assigned to the individual. Because of poor digestions, *Nde* I genotype data were available for only 112 individuals, but these specimens represented all sampling locations. The Jamaican population was fixed for the *Nde* I "B" genotype, and the "C" genotype predominated in all other populations. Only two additional *Nde* I variants, present in one individual each, were observed; thus, in our analyses we assigned the common "C" genotype to the 58 individuals not scored for *Nde* I.

In most of the first 55 samples surveyed, *Cla* I revealed a single restriction site, and *Nco* I revealed no sites. Thus, we analyzed most individuals, including representatives of all populations, with these enzymes through double digests: 122 individuals (of 170) with *Cla* I and *Sac* I; 121 individuals with *Nco* I and *Dra* I. Furthermore, 128 individuals were surveyed by double digests with *EcoR* I and *Pst* I; this allowed better resolution of a small size difference in the large *Pst* I fragment. We also made a very large number of side-by-side comparisons of fragment profiles for single- and double-enzyme digestions to verify size homology of specific restriction fragments.
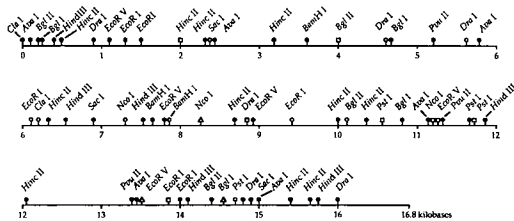
For most enzymes, restriction-fragment pro-



FIG. 2. Restriction-site maps for two *Coereba flaveola* mtDNA haplotypes. ●, sites present in both haplotypes; □, sites present only in the Puerto Rican haplotype; △sites present only in the Venzuelan haplotype; ○, additional sites found in other haplotypes. *Nde* I and *Stu* I sites and a few sites for other enzymes were not mapped (see text).

files were easily related to one another by assuming the gains or losses of single restriction sites (e.g., fig. 3). Using the map data and fragment data from single-enzyme digestions, we were able to infer restriction sites with confidence for all enzymes and individuals not physically mapped (Bermingham 1990). Thus, all analyses were based on restriction sites rather than fragment lengths. Data were summarized using REAP (McElroy et al. 1992) to calculate indices of nucleotide diversity ($\pi$) and divergence ($d_{xy}$) described by Nei and coworkers (Nei and Tajima 1983; Nei 1987; Nei and Miller 1990). We used a maximum-likelihood approach to calculate the expected number of nucleotide substitutions per nucleotide site; associated standard errors were calculated following Nei and Tajima (1983). Neighbor-joining (NJ; Saitou and Nei 1987) and UPGMA (Sneath and Sokal 1973) clustering of haplotypes were performed using the NTSYS package (Rohlf 1990), and a consensus of minimum-distance mtDNA haplotype trees was produced using PAUP (Swofford 1993). For the latter analysis we used a heuristic search with the haplotypes added at random and branches were swapped using the tree dissection-reconnection procedure (see Swofford 1993). A strict consensus tree was produced from the first 1000 equally most parsimonious trees found in each of three independent runs; those trees were identical.

### RESULTS

*Restriction-Site Analysis.* —We used 16 restriction enzymes to analyze the mitochondrial genomes of 170 bananaquits sampled from 12 Caribbean islands, five continental sites in Costa Rica, Panama and Venzuela, and one land-bridge island in the Pearl Archipelago of the Gulf of
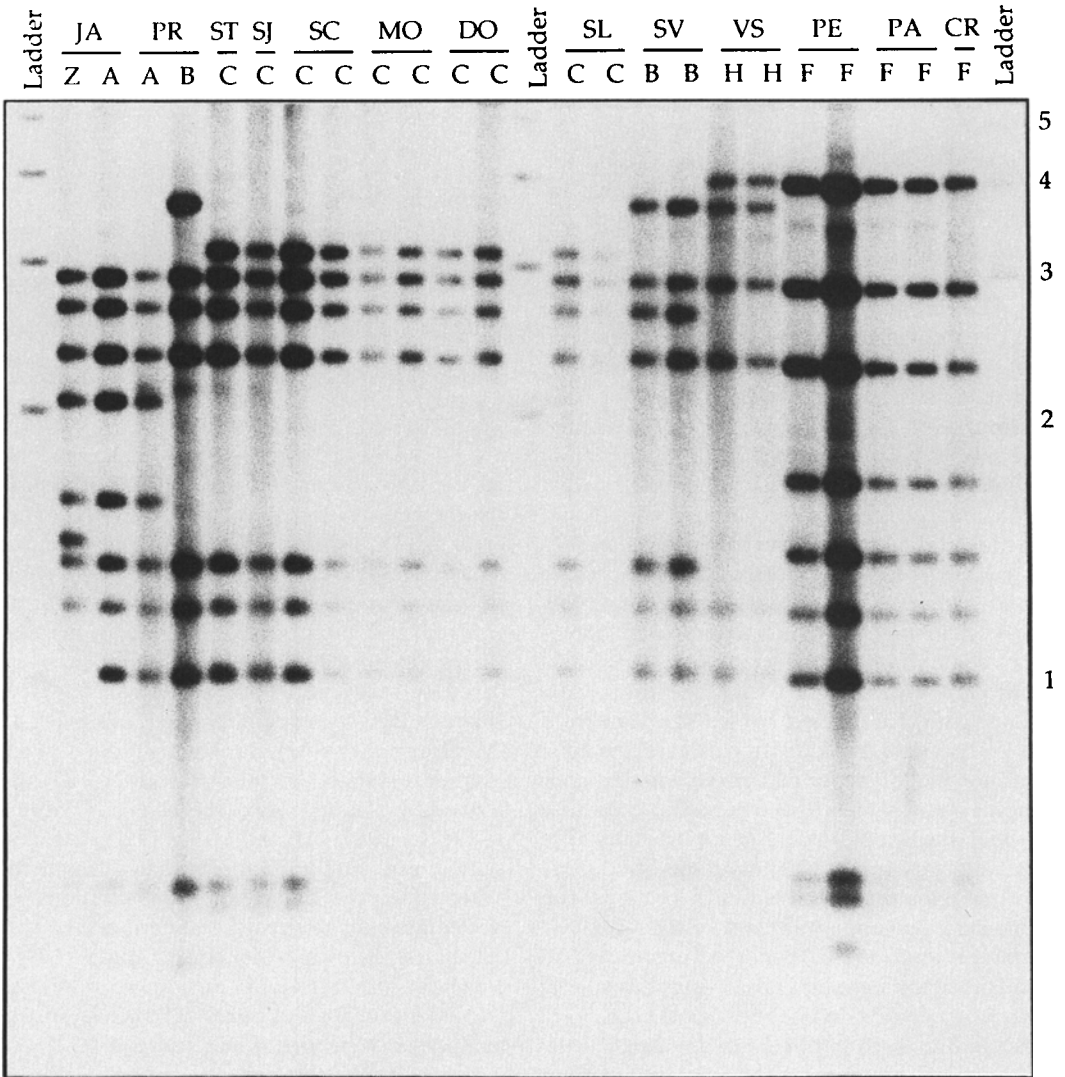
FIG. 3. Restriction-fragment-length-polymorphism analysis of *Coereba flaveola* from various localities around the Caribbean basin, using the endonuclease *Stu* I. Two-letter acronyms at the top refer to sampling localities as presented in table 1; single letters below refer to restriction-site patterns. A 1-kilobase ladder was used as a molecular size marker.

Panama (table 1, fig. 1). Fifty-eight mtDNA haplotypes were observed (table 2), and for two of those (PR12 and VE7) most restriction sites were physically mapped (fig. 2). A total of 108 sites were identified, representing 3.8% of the approximately 16.8 kilobase pair bananaquit mtDNA genome. On the average, 66 sites were assayed for each individual, of which 46 were shared by all bananaquits. No obvious mtDNA size variation was noted across the birds surveyed; we did, however, observe one possible example of *Hinc* II restriction-site heteroplasmy in our unique sample from Costa Rica.

*MtDNA Relationships among Populations.* — Multiple fixed restriction-site differences genetically defined six regional bananaquit populations (fig. 4): Jamaica (JA), Central America (Costa Rica and Panama; hereafter CA), Venezuela (VE), southern Lesser Antilles (Grenada and St. Vincent; GSV), north-central Lesser Antilles and the U.S. Virgin Islands (St. Lucia to St. Thomas; LA), and Puerto Rico (PR). In most cases, the geographic structuring of mtDNA variation was well documented in neighbor-joining (fig. 5), UPGMA (results not shown) and Wagner

TABLE 2. Geographical origin and frequency of occurrence of mtDNA haplotypes in *Coereba flaveola*. Codes for sample sites are from table 1, and locations are shown in fig. 1. Letters indicate restriction-site patterns corresponding to the following enzymes: *Bam*H I, *Bgl* I, *Bgl* II, *Cla* I, *Dra* I, *Eco*R I, *Eco*R V, *Hin*d III, *Nco* I, *Nde* I, *Pst* I, *Pvu* II, *Sac* I, *Stu* I, *Ava* I, and *Hinc* II.

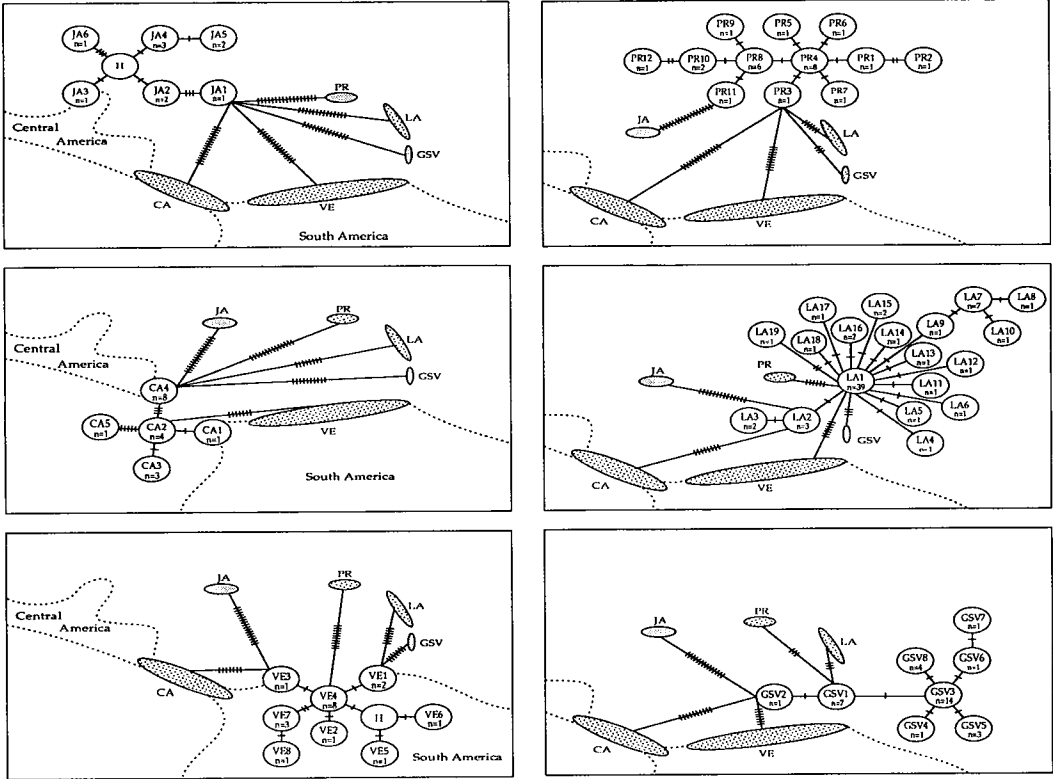| | | JA | PR | ST | SJ | SC | MO | GU | DO | MA | SL | SV | GR | VS | VD | VF | PA | PE | CR | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| JA1 | ABCDCCCBCBDECADL | 1 | | | | | | | | | | | | | | | | | | 1 |
| JA2 | ABCDCFGBCBDECZDL | 2 | | | | | | | | | | | | | | | | | | 2 |
| JA3 | ABCDCFGBCBDECYDM | 1 | | | | | | | | | | | | | | | | | | 1 |
| JA4 | ABCECFGBCBDECZDM | 3 | | | | | | | | | | | | | | | | | | 3 |
| JA5 | ABCECEGBCBDECZDM | 2 | | | | | | | | | | | | | | | | | | 2 |
| JA6 | ABCCCFGACBDECZCM | 1 | | | | | | | | | | | | | | | | | | 1 |
| PR1 | CBDCCCECCCCCCBCD | | 1 | | | | | | | | | | | | | | | | | 1 |
| PR2 | CBDCCCEDCCCCCBCE | | 1 | | | | | | | | | | | | | | | | | 1 |
| PR3 | CBDCCDECCCCCCBCC | | 1 | | | | | | | | | | | | | | | | | 1 |
| PR4 | CBDCCDECCCCCCBCD | | 8 | | | | | | | | | | | | | | | | | 8 |
| PR5 | CBDCCDECCCCCCBCF | | 1 | | | | | | | | | | | | | | | | | 1 |
| PR6 | CBDCCDECCCCCCBCI | | 1 | | | | | | | | | | | | | | | | | 1 |
| PR7 | CBDCCDECCCCCCBBD | | 1 | | | | | | | | | | | | | | | | | 1 |
| PR8 | CBDCCDECCCCCCACD | | 6 | | | | | | | | | | | | | | | | | 6 |
| PR9 | CBDCCDECCACCCACD | | 1 | | | | | | | | | | | | | | | | | 1 |
| PR10 | CBDCCDECCCCECACD | | 2 | | | | | | | | | | | | | | | | | 2 |
| PR11 | CBDCCDICCCCCCACD | | 1 | | | | | | | | | | | | | | | | | 1 |
| PR12 | CBDCEDECCCCECACC | | 1 | | | | | | | | | | | | | | | | | 1 |
| LA1 | CCCCCCCCCCCCCCCC | | | | | 8 | 5 | 6 | 8 | 3 | 9 | | | | | | | | | 39 |
| LA2 | BCCCCCCCCCCCCCCC | | | | | | | | 1 | 2 | | | | | | | | | | 3 |
| LA3 | BCCCDCCCCCCCCCCC | | | | | | | 2 | | | | | | | | | | | | 2 |
| LA4 | CCCCDCCCCCCCCCCC | | | | | | | | | 1 | | | | | | | | | | 1 |
| LA5 | CCCCFCCCCCCCCCCC | | | | | | | | | | 1 | | | | | | | | | 1 |
| LA6 | CDCCCCCCCCCCCCCC | | | | 1 | | | | | | | | | | | | | | | 1 |
| LA7 | CDCCCCGCCCCCCCCC | | | | | | | | 4 | 2 | 1 | | | | | | | | | 7 |
| LA8 | CDCCCCGCCCCCCCCW | | | | | | | | 1 | | | | | | | | | | | 1 |
| LA9 | CCCCCCGCCCCCCCCC | | | | | | | | | 1 | | | | | | | | | | 1 |
| LA10 | CDCCCDGCCCCCCCCC | | | | | | | | 1 | | | | | | | | | | | 1 |
| LA11 | CCCCCCCECCCCCCCC | | | | | | | | | | 1 | | | | | | | | | 1 |
| LA12 | CCCCCCCBCCCCCCCC | | | | | | 1 | | | | | | | | | | | | | 1 |
| LA13 | CCCCCCCCDCCCCCCC | | | | | | | | | 1 | | | | | | | | | | 1 |
| LA14 | CCCCCCCCCCBCCCCC | | | | | | | | | | 1 | | | | | | | | | 1 |
| LA15 | CCCCCCCCCCBCCCCC | | | | | | 1 | | | | 1 | | | | | | | | | 2 |
| LA16 | CCCCCCCCCCCCDCC | | | | | | | | 2 | | | | | | | | | | | 2 |
| LA17 | CCCCCCCCCCCCCCG | | | 1 | | | | | | | | | | | | | | | | 1 |
| LA18 | CCCCCCCCCCCCCCCH | | | | | | | | | | | 1 | | | | | | | | 1 |
| LA19 | CECCECCCCCCCCCCC | | | | | | | | | | | 1 | | | | | | | | 1 |
| GSV1 | CBCCCCDCCCCCCBCC | | | | | | | | | | | 5 | 2 | | | | | | | 7 |
| GSV2 | CBCCCCDCCCCCCBCZ | | | | | | | | | | | 1 | | | | | | | | 1 |
| GSV3 | CBCCCCDCCCCDCBCC | | | | | | | | | | | 3 | 11 | | | | | | | 14 |
| GSV4 | CBCCCCECCCCDCBCC | | | | | | | | | | | 1 | | | | | | | | 1 |
| GSV5 | CBCCCCDCCCCDCBCB | | | | | | | | | | | 3 | | | | | | | | 3 |
| GSV6 | CBCCCCDCCCCDDBCC | | | | | | | | | | | 1 | | | | | | | | 1 |
| GSV7 | CBCCCCCCCCCDDBCC | | | | | | | | | | | 1 | | | | | | | | 1 |
| GSV8 | CBCCCCDCCCCFCBCC | | | | | | | | | | | | 4 | | | | | | | 4 |
| VE1 | CCCCCCFCDCBCCHDZ | | | | | | | | | | | | | 2 | | | | | | 2 |
| VE2 | CCCCCCHCDCBCCIDZ | | | | | | | | | | | | | 1 | | | | | | 1 |
| VE3 | BCCCCCHCDCBCCHDZ | | | | | | | | | | | | | 1 | | | | | | 1 |
| VE4 | CCCCCCHCDCBCCHDZ | | | | | | | | | | | | | 6 | 2 | | | | | 8 |
| VE5 | DCCCCCHFDCBCCHDZ | | | | | | | | | | | | | 1 | | | | | | 1 |
| VE6 | CCCCCCHFECBCCHDZ | | | | | | | | | | | | | 1 | | | | | | 1 |
| VE7 | CCCCCCHCECACCHDZ | | | | | | | | | | | | | | | 3 | | | | 3 |
| VE8 | CGCCCCHCECACCHDZ | | | | | | | | | | | | | | | 1 | | | | 1 |
| CA1 | BBECCCFCCCBCCGDX | | | | | | | | | | | | | | | | 1 | | | 1 |
| CA2 | BBECCCFCCCBCCFDX | | | | | | | | | | | | | | | | 4 | | | 4 |
| CA3 | BBECCCFCCCBDCFDX | | | | | | | | | | | | | | | | 3 | | | 3 |
| CA4 | BBECCCFCCCBCCFCA | | | | | | | | | | | | | | | | | 8 | | 8 |
| CA5 | CFECCCFCCCBCCFEZ | | | | | | | | | | | | | | | | | | 1 | 1 |

FIG. 4. Relationships between mtDNA haplotypes within groups of populations identified on the basis of multiple restriction-site differences (see text). Minimal distance between groups of populations are also shown. Each tic mark represents the loss or gain of a restriction site.

parsimony (fig. 6) analyses. However, these analyses were not in full agreement regarding the relationships of the three Antillean population groups (PR, LA, and GSV; see below).

The mtDNA clade representing the 10 Jamaican individuals was the most divergent; six fixed restriction-site differences distinguished the Jamaican bananaquits from all others. In pairwise comparisons between Jamaican birds and all other samples, we observed a minimum of 15 restriction-site changes (fig. 4), and an estimated mean mtDNA sequence divergence ($d_{xy}$) of 0.029 (range 0.027–0.035). In birds, such levels of differentiation are typical of interspecific relationships (see table 3 in Seutin et al. 1993). Numerical analyses, assuming a mid-point root, further indicated that a continental mtDNA clade, rather than the Jamaican clade, was the sister taxon to a clade comprised of the three eastern Antillean mtDNA haplotype groups (PR, LA, GSV; figs. 5, 6). The mean mtDNA sequence divergence separating continental from all eastern An-

tillean bananaquit populations was 0.014 (range 0.011–0.022), a mean value identical to that observed between the Panama and Venezuela populations. These levels of divergence are higher than those typically observed between conspecific avian populations and are closer to levels seen between closely related species (Avise and Zink 1988; Seutin et al. in press).

Within Panama, a minimum of three restriction-site differences distinguished the single mtDNA haplotype carried by the eight Pearl Islands bananaquits (*C. f. cerinoclunis*) from the three haplotypes assayed in the eight birds from Bocas del Toro (*C. f. mexicana;* fig. 4); the mean genetic distance ($d_{xy}$) between these populations was 0.004. A minimum of five site differences were inferred between bananaquits from Bocas del Toro and our unique Costa Rica specimen, which all belong to the *mexicana* subspecies. Thus, mtDNA differentiation was higher among individuals within the *mexicana* subspecies than it was between this and the *cerinoclunis* subspe-
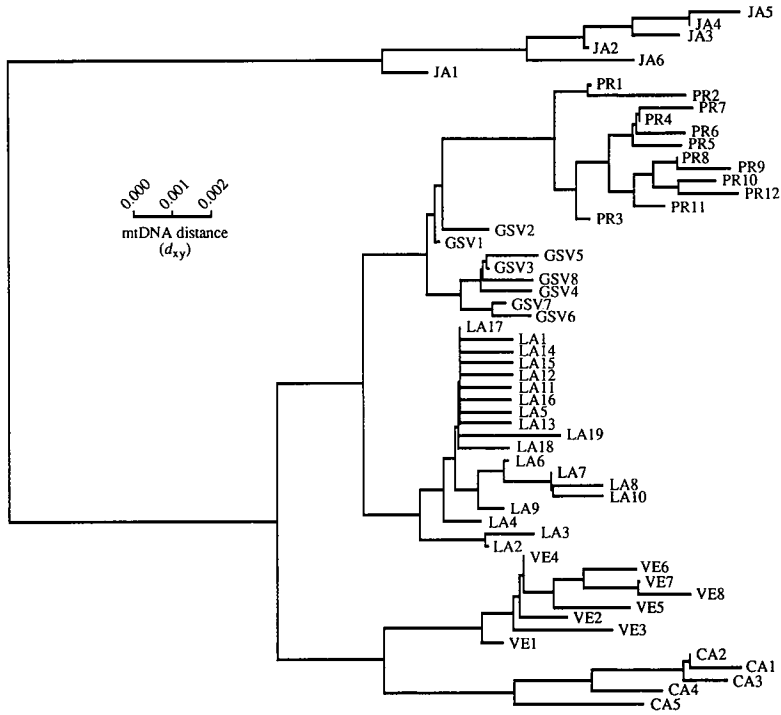
FIG. 5. Neighbor-joining cluster analysis of 58 *Coereba flaveola* mtDNA haplotypes.

cies. Within Venezuela (*C. f. luteola*), the two individuals collected in the Estado de Falcon had the same mtDNA haplotype (VE4) as six individuals from Estado de Sucre. However, mtDNA haplotypes from individuals collected in the Distrito Federal (VE7 and VE8) differed by a minimum of two restriction sites ($d_{xy}$) = 0.003; fig. 4) from all other VE haplotypes. Sampling localities in Falcon and Sucre were coastal and at sea level; our collecting site in the Distrito Federal, which lies between Estado de Falcon and Estado de Sucre, was inland and at an altitude of 600 m.

Within the eastern Antilles, the three geographic units defined earlier (PR, LA, and GSV) shared no mtDNA haplotypes among themselves or with other population groups. This clearly indicates the genetic distinctiveness of those regional populations, but their phylogenetic relationships could not be clearly determined either through the analysis of haplotype relationships (fig. 4) or by numerical analyses (fig. 5, 6). This probably resulted from the similar minimum numbers of site differences distinguishing these three groups (PR–LA, 6; PR–GSV, 3; LA–GSV, 3), and the existence of several ho-

moplasious characters in the restriction-site data set. Mean mtDNA distances ($d_{xy}$) between the three groups were PR–LA, 0.009; PR–GSV, 0.006; LA–GSV, 0.005.

The limited geographic distribution of mtDNA haplotypes found in Puerto Rico, Grenada and St. Vincent, Jamaica, and most continental locations contrasted sharply with the widespread distribution of north-central Antillean (LA) mtDNA haplotypes. The numerically predominant LA haplotype (LA1), observed in 39 of the 68 samples collected from the region (table 2), was in high frequency or fixed on all islands from St. Lucia north to St. Croix (subspecies *martinicana, bartholemica,* and *newtoni*). Other LA mtDNAs found in two or more individuals had more restricted distributions (table 2); for example, the second most numerous LA mtDNA haplotype (LA7), seen in seven individuals, was restricted to St. Lucia, Martinique, and Dominica (subspecies *martinicana* and *bartholemica*). There were no fixed differences between St. Lucia, Martinique, and Dominica and the unique haplotypes on each of the islands had frequencies that were too low to reject the hypothesis that the three islands represent either a single pan-
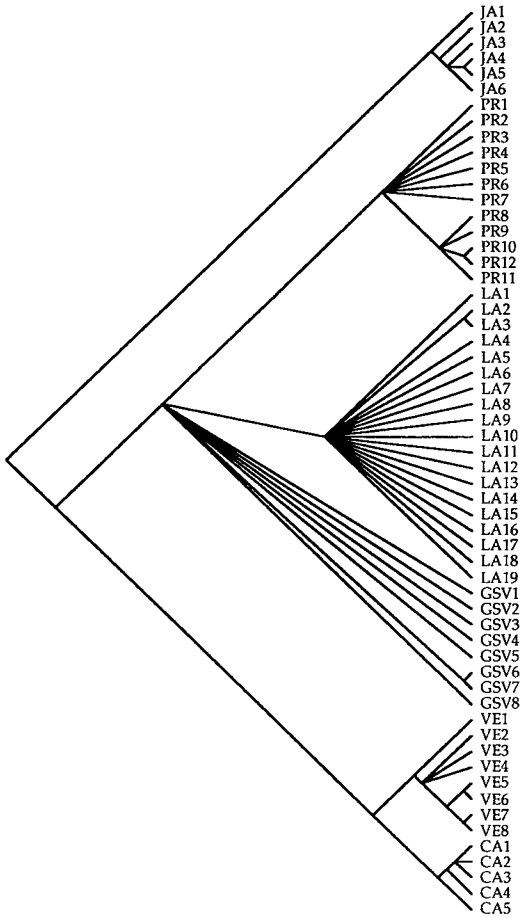
FIG. 6.    Strict consensus of unrooted Wagner parsimony trees (length: 98; CI: 0.622) of the relationships among 58 *Coereba flaveola* mtDNA haplotypes.

types and large geographic distances within islands. Nonetheless, certain island samples (i.e., Jamaica, Puerto Rico, St. Lucia, and St. Vincent) comprised individuals collected over much of the island or over a wide range of altitudes.

Jamaica had both the highest mtDNA haplotype and nucleotide diversity (0.89 and 0.0037, respectively), and St. Croix had both the lowest estimated mtDNA haplotype and nucleotide diversity (0.38 and 0.0005, respectively). The other populations had roughly similar diversity values (table 1). Island area and both mtDNA haplotype and nucleotide diversity were significantly related (Kendall's rank correlations; in both cases: $\tau$ = 0.810, $P$ = 0.011). Klein (1992) also found island area and haplotype diversity to be correlated in the yellow warbler. Overall, intrapopulation mtDNA variability in *C. flaveola* was similar to levels observed in other tropical avian species. Seutin et al. (1993) reported that nucleotide diversity in five insular populations of *Saltator albicollis* ranged from 0.0000 to 0.0028, and was 0.0017 in a mainland population. Most values for bananaquits are in the range reported for local populations of continental North American passerines (0.0008–0.0027; summarized in Seutin et al. 1993, in press).

We observed reduced mtDNA variability in two groups of bananaquits. The eight assayed individuals from Isla Chapera, in the Pearl Islands, Gulf of Panama, carried a single mtDNA haplotype (table 2). Isla Chapera has been isolated from the mainland of Panama for less than 10,000 yr (Bartlett and Barghoorn 1973; Fairbanks 1989) and supports a large population of bananaquits assigned to a subspecies endemic to the Pearl Archipelago (*C. f. cerinoclunis;* Wetmore et al. 1984). Reduced genetic variability in the Chapera population could be due either to recent colonization of the island by a small founder population or, more probably, the loss of haplotype diversity through genetic drift.

Reduced mtDNA variability was also noted in the northern LA islands (St. Croix south to Guadeloupe): St. Croix had both the lowest estimated mtDNA haplotype and nucleotide diversity (table 1), and we observed no variation in the combined samples from Guadeloupe (six individuals) and adjacent Montserrat (five individuals). The probability of sampling by chance 11 LA1 haplotypes from a population showing the levels of variability seen in Dominica, Martinique, and St. Lucia (frequency of LA1, 0.44) is only 0.0001. Because Guadeloupe is the largest

mictic population or a recent range expansion within the Lesser Antilles, as we had previously inferred for *Saltator albicollis* (Seutin et al. 1993). One mtDNA haplotype (LA15) was assayed in two bananaquits collected from the two ends of the region (St. Lucia and St. Croix). The single birds sampled on St. Thomas and St. John each had a unique mtDNA haplotype, but these differed from the common LA haplotype by only one restriction site.

*MtDNA Diversity within Island and Mainland Populations.* — We sampled 10 or more individuals from each of seven islands and one mainland location (table 1) and restricted our analysis of haplotype and nucleotide diversity to these eight sites. Because our study focused on larger-scale patterns of geographic variation in bananaquits, we did not attempt to collect birds across habitat

of the Lesser Antillean islands, its apparent reduced mtDNA variability is most readily explained by a founder effect resulting from recent colonization or from a post-founding bottleneck.

On Grenada and St. Vincent, our collections included both the light-phase ($n = 9$) and dark-phase ($n = 22$) bananaquits. There was no relationship between mtDNA haplotype and bananaquit color phase, whether the island samples were considered separately (for Grenada: $G = 2.316$, df = 2, $P > 0.25$; for St. Vincent: $G = 3.165$, df = 3, $P > 0.30$) or jointly ($G = 5.222$, df = 4, $P > 0.25$).

## DISCUSSION

Our study of mtDNA polymorphism among Caribbean bananaquits revealed a degree of phylogeographic structuring and divergence among populations that was high by avian standards. The geographic distribution of bananaquit mtDNA haplotypes indicates that the species has had a complex history in the Caribbean region. Our results suggest that certain island populations underwent phases of geographic expansion within the Antilles, possibly following either extinction in parts of the range, the competitive exclusion of local populations by invaders, or the replacement of local haplotypes through introgression. Colonization of the continental mainland from the West Indies cannot be rejected by our data. We consider these issues in more detail below.

*Taxonomic Distinctions and Genetic Divergence.* — As Banks and Hole (1991) pointed out, early taxonomic work on Caribbean birds "was based mainly on small samples from island populations in an age when supposed isolation led to the expectation of differentiation, and when individual variation within populations was not taken into account." On closer examination, they found little morphological support for the many named subspecies of the mangrove cuckoo (*Coccyzus minor*) in the West Indies and suggested that the species has been highly vagile within the archipelago, its movement aided by hurricanes and storms.

On the other hand, in the bananaquit, which in the West Indies occupies much of the same geographical range and habitats as the mangrove cuckoo, there was mtDNA support for genetic distinctiveness of some of the named subspecies. For example, fixed restriction-site differences separate the subspecies *flaveola* (Jamaica) and *portoricensis* (Puerto Rico) from one another and

from all other subspecies studied. Furthermore, we discovered no cases where the mtDNA data were inconsistent with named subspecies, although the other West Indian mtDNA groupings (GSV and LA) encompassed two and four subspecies, respectively (table 1). To the degree that mtDNA in these bananaquits evolves in a roughly clocklike manner, it appears that not all named subspecies are historically and evolutionarily equivalent. This has important consequences for the study of biogeographic patterns. For instance, in the characterization of the so-called taxon cycle for Antillean birds, Ricklefs and Cox (1972) relied on taxonomic distinctions as indicators of evolutionary divergence and the age of island populations. Genetic analyses will undoubtedly modify this and other biogeographic characterizations.

An important finding of our study is that levels of mtDNA differentiation between regional groups of bananaquit populations were higher and showed greater phylogeographic structure than those typically observed among avian conspecifics in temperate regions. Data showing elevated genetic divergence among populations of Neotropical birds have now been obtained for species representing a wide range of unrelated passerine families (Capparella 1988; Hackett and Rosenberg 1990; Escalante-Pliego 1991; Peterson et al. 1992; Seutin et al. 1993; this study) suggesting that the tendency is generalized in tropical species and due not only to taxon-specific variation in rates of mtDNA and protein evolution. Other factors, such as decreased vagility, more stable population sizes, and possibly lower rates of population extinction in the tropics, have to be considered. A careful assessment of the generality and details of increased phylogeographic structuring of tropical bird populations is likely to modify our understanding of the process of avifaunal diversification.

*The Origin of West Indian Bananaquit Populations.* — Of the bananaquit populations that we sampled, the Jamaican is the most distinctive, and it is almost equally differentiated from all other populations (fig. 4). Without samples from other Greater Antillean and continental populations we cannot resolve its history. Additional data might distinguish whether the Jamaican population is part of an older West Indian taxon that is ancestral to all other bananaquit clades, or whether it represents an older invasion of the West Indies from established continental populations. All the other populations that we studied

clearly belong to a clade of *C. flaveola* that diversified subsequent to the isolation of the Jamaican population.

Three groups of bananaquit populations, representing southern Central America, northern Venezuela, and the eastern Antilles taken as a whole (Puerto Rico to Grenada), are approximately equally differentiated from each other (average $d_{xy} = 0.014$; figs. 4, 5). Assuming that mtDNA sequences of these birds diverge at a rate of approximately 2% per million years (e.g., Brown et al. 1979; Shields and Wilson 1987; but see Avise et al. 1992; Martin et al. 1992), these groups became isolated less than 1 mya. The almost equal levels of divergence between these groups suggest that they may be products of a single range expansion. With other models of dispersal (e.g., sequential stepping-stone, nonsynchronized invasions from a single source, independent invasions from differentiated sources), a hierarchy of relationships between groups would be expected.

Judging from the distinctiveness of the Jamaican bananaquit population and the absence of the species from the Yucatán Peninsula and Cuba, it appears more likely that the colonization of the eastern Caribbean islands proceeded from South America rather than from northern Central America through the Greater Antilles. Alternatively, the expansion may have originated in the West Indies and spread to the continent. More extensive sampling, especially in South America and northern Central America, should help resolve these possibilities.

*History of the Bananaquit in the Antilles.*— Within the eastern Antilles, three geographically restricted groups of haplotypes were identified on the basis of multiple mtDNA restriction-site differences (fig. 4): Puerto Rico (PR); north-central Lesser Antillean islands (the U.S. Virgin Islands south to St. Lucia; LA); and Grenada–St. Vincent (GSV). Distance and parsimony analyses (figs. 5, 6) did not clearly resolve evolutionary relationships among these groups, probably because of the presence of homoplasious characters.

A number of historical scenarios relating the Antillean groups of haplotypes are thus possible. The simplest begins with the spread of an ancestral eastern Antillean population throughout the West Indies, at least as far as Puerto Rico, but not so far as Jamaica. The island populations then began to diversify, producing distinctive haplotypes on each of the islands. Exposure of

the Grenada Bank probably to within 10 km of St. Vincent during Pleistocene periods of low sea level (Fairbanks 1989; Pregill and Olson 1981) allowed gene flow between these islands at times, accounting for their present genetic closeness. To the north, the genetic homogeneity of the populations between St. Lucia and the U.S. Virgin Islands suggests a relatively recent spread of a specific north-central Lesser Antillean haplotype through most of those islands. Replacement of older mtDNA haplotypes could have occurred through lineage sorting associated with introgression, or through the competitive exclusion of local populations by invaders; alternatively the colonizers may have replaced island populations that had previously gone extinct.

If founder effects resulting in reduced within-population genotypic variability accompany colonization, the pattern of haplotypic diversity in the north-central Lesser Antillean islands suggests that the later spread of *C. flaveola* within the Lesser Antilles occurred in two waves: an older one in the southern islands (St. Lucia, Martinique, Dominica), which now show moderate levels of mtDNA variability, and a more recent progression, probably from Dominica, through the northern islands (Guadeloupe through St. Croix and the Virgin Islands), which today still show little mtDNA variation. Reduced mtDNA variability on Montserrat and St. Croix may also be associated, at least in part, with the probable smaller size of the populations on those small islands.

Alternatively, there may not have been *C. flaveola* populations in the northern Lesser Antilles until recently. During an ancient expansion, the species may have bypassed these islands and reached Puerto Rico directly from the southern end of the archipelago.

*Invasiveness and Invasibility.*—Our analyses of mtDNA variation indicated that *C. flaveola* is not highly vagile within the West Indies as fixed genotypic differences often are maintained between adjacent islands. Multiple fixed restriction-site differences were also found between continental populations separated by only a few hundred kilometers, suggesting that reduced vagility is also characteristic of continental bananaquit populations.

A remarkable feature of this data is the mtDNA distance observed between bananaquits on Puerto Rico and those on the U.S. Virgin Islands, in spite of the land connection that united these sites within the past 20,000 years. The banana-

quit population on St. Croix clearly belongs to a north-central Lesser Antillean mtDNA clade, as apparently do those of St. John and St. Thomas. Those three populations probably represent the end point of a wave of expansion of central Lesser Antillean birds through the small islands of the northern Lesser Antilles (e.g., Nevis, St. Kitts, St-Barthélémy, St. Maarten and Anguilla). After having successfully colonized those islands, there is no evidence of these birds continuing to colonize across the short distance between the U.S. Virgin Islands and Puerto Rico.

To explain the apparent absence of Puerto Rican mtDNA haplotypes in the U.S. Virgin Islands, it is possible (e.g., Banks and Hole 1991) that dispersal within the West Indies occurs mostly from south and east to north and west because of the prevailing winds and the general direction of hurricanes. However, depending on the track of the center of a hurricane, winds between two relatively close points may blow either direction. Thus, we have no simple explanation for the lack of Puerto Rican mtDNA haplotypes on islands to the east and south.

The fact that Lesser Antillean bananaquits did not expand to Puerto Rico from the U.S. Virgin Islands suggests that invasion from a small land mass to a larger one is difficult. This idea is supported by the observation that Bahamian bananaquits have not invaded Cuba, even though they occur on small keys to the north (e.g., Cayo Coco), and that populations in the far western Caribbean (*C. f. caboti*) have not invaded the Yucatán Peninsula. Considering the ability of bananaquits to establish populations on small islands across substantial oceanic distances, it is unlikely that failure to colonize results from a lack of migrants. There have been many cases of vagrants reported outside the normal range (Bond 1963, 1979) and flying at sea.

We believe it is unlikely that bananaquits are absent from Cuba and the Yucatán Peninsula because of unsuitable physical conditions or the presence of strong competitors. The environment of eastern Cuba (Oriente Province) resembles that of Hispaniola and Jamaica, where the species is abundant. Like most of the Caribbean islands Cuba has fewer species of potential competitors than continental Central and South America, over which the bananaquit is widely distributed. Within the Greater Antilles the bananaquit is one of the most abundant landbirds (e.g., Lack 1976; Cox and Ricklefs 1977). A disease organism present on Cuba may prevent the

establishment of *C. flaveola*. Avian malaria and pox have been implicated in the extinction of many native Hawaiian birds (Warner 1968; Van Riper et al. 1986). Susceptibility or resistance to haematozoa appears to vary among species of Lesser Antillean passerines and perhaps even among island populations of the same species (V. Apanius et al. unpubl. data). Cuban native species may harbor strains of disease organisms to which bananaquit colonizers are susceptible. The possible role of disease organisms in constraining the geographic distribution of the bananaquit and other insular birds deserves attention.

The geographical distribution of mtDNA haplotypes, and more generally that of the populations of bananaquits in the West Indies, suggest that populations may go through phases of invasiveness, as north-central Antillean birds appear to have done recently, and relative geographic quiescence, as evidenced by the birds of Puerto Rico and those of Grenada and St. Vincent. We concluded earlier (Seutin et al. 1993), from an analysis of mtDNA variability in insular and continental populations of the streaked saltator, that an Antillean population of this species, after a long period of isolation in the archipelago, has probably recently expanded its range through at least three of the four islands now occupied by the taxon. Genetic analyses of additional insular bird species will be required to assess the generality of a pattern of alternation between geographical expansion and quiescence within archipelagoes. Nevertheless, these data suggest that different populations of the same species may be in different phases of colonizing activity at a specific time, a possibility that was not considered in the theoretical development of taxon cycles (Wilson 1961; Ricklefs and Cox 1972).

In summary, our study of mtDNA variation in Caribbean bananaquits revealed greater phylogeographic structure than has been observed in other avian species studied thus far. In addition, levels of mtDNA divergence among regional populations of bananaquits were generally higher than those found among conspecific temperate bird populations. Hence, generalizations concerning population genetic architecture in birds (i.e., low-to-moderate levels of genetic divergence among conspecifics and low-to-moderate geographic structuring of the variation present) have probably been biased by an almost exclusive focus on temperate species. Furthermore, our studies of Caribbean birds have in-

dicated that taxonomic distinctions are, at best, only loosely correlated with genetic distance, suggesting that presently recognized Antillean bird subspecies should not be considered of equivalent phylogenetic rank in historical biogeographic analyses.

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Size of mitochondrial DNA restriction fragments produced by 16 enzymes used in the analysis of 17 *Coereba flaveola*. Single letter acronyms for fragment patterns are those used in table 2. Sizes are in base pairs. Sum of fragment sizes is given when appropriate. BYSUB, large fragment; —, fragment absent; NV, fragment not visualized.

*Ava* I

| B | C | D | E | F |
|---|---|---|---|---|
| 5300 | 5300 | 5300 | 5300 | 5300 |
| 3800 | — | — | — | 3800 |
| 3450 | 3450 | — | — | — |
| — | — | 3000 | 3000 | 3000 |
| 2330 | 2330 | 2330 | 2330 | 2330 |
| — | 2100 | 2100 | 2100 | — |
| 1900 | 1900 | 1900 | 1900 | 1900 |
| — | 1750 | 1750 | — | — |
| — | — | — | 1600 | — |
| — | — | 420 | 420 | 420 |
| — | — | — | NV | — |
| 16,780 | 16,830 | 16,800 | 16,650 | 16,750 |

*Bam*H I

| A | B | C | D |
|---|---|---|---|
| — | BYSUB | — | — |
| — | — | BYSUB | — |
| BYSUB | — | — | — |
| — | — | — | BYSUB |
| 4200 | — | — | — |
| — | — | 4050 | 4050 |
| — | — | — | 1800 |
| 210 | 210 | — | — |

*Bgl* I

| B | C | D | E | F | G |
|---|---|---|---|---|---|
| 6350 | — | — | — | 6350 | — |
| 6100 | 6100 | — | 6100 | — | 6100 |
| 4400 | 4400 | 4400 | 4400 | 4400 | — |
| — | — | 4050 | — | 4050 | — |
| — | 3800 | 3800 | — | — | 3800 |
| — | — | — | — | — | 3000 |
| — | 2550 | 2550 | 2550 | — | 2550 |
| — | — | — | 2350 | — | — |
| — | — | 1950 | — | 1950 | — |
| — | — | — | 1300 | — | 1300 |
| 16,850 | 16,850 | 16,750 | 16,700 | 16,750 | 16,750 |

*Bgl* II

| C | D | E |
|---|---|---|
| BYSUB | — | — |
| — | BYSUB | — |
| — | — | BYSUB |
| — | — | 4200 |
| — | 3800 | — |
| 2700 | 2700 | 2700 |

*Cla* I

| C | D | E |
|---|---|---|
| BYSUB | — | — |
| — | BYSUB | BYSUB |
| — | 6200 | — |
| — | — | 3600 |
| — | — | 2500 |

*Dra* I

| C | D | E | F |
|---|---|---|---|
| BYSUB | — | — | — |
| — | 9800 | — | — |
| — | — | — | 8500 |
| — | — | 7900 | — |
| — | — | 6000 | — |
| — | — | — | 4800 |
| — | 3700 | — | — |
| 1800 | 1800 | 1800 | 1800 |
| 1170 | 1170 | 1170 | 1170 |
| | 16,470 | 16,870 | 16,270 |

*Eco*R I

| C | D | E | F |
|---|---|---|---|
| BYSUB | — | — | — |
| — | BYSUB | — | — |
| — | — | — | 7300 |
| — | — | 4600 | 4600 |
| — | — | 4300 | — |
| 4200 | 4200 | 4200 | 4200 |
| — | — | 3300 | — |
| 210 | 210 | 210 | 210 |
| — | 165 | — | — |
| | | 16,610 | 16,310 |

*Eco*R V

| C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|
| BYSUB | — | — | — | BYSUB | — | BYSUB |
| 7300 | 7300 | — | 7300 | — | — | — |
| — | 6900 | 6900 | — | — | — | — |
| — | — | 6700 | — | — | 6700 | 6700 |
| — | — | — | 4650 | — | 4650 | — |
| — | — | — | 4600 | — | 4600 | — |
| — | — | — | — | 3950 | — | — |
| — | — | — | — | 3350 | — | — |
| — | 2300 | 2300 | — | — | — | — |
| — | — | 675 | — | — | 675 | 675 |
| | 16,500 | 16,575 | 16,550 | | 16,625 | |

*Hinc* II

| W | X | Y | Z | A | B | C | D | E | F | G | H | I | L | M |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| — | — | — | — | — | — | — | — | — | — | — | — | — | 5300 | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — | — | 3650 |
| — | 3550 | 3550 | 3550 | 3550 | — | — | — | 3550 | — | — | — | — | 3550 | 3550 |
| — | — | — | — | — | — | — | — | — | — | 3450 | — | — | — | — |
| — | 3350 | — | 3350 | 3350 | 3350 | 3350 | 3350 | 3350 | 3350 | 3350 | 3350 | 3350 | 3350 | 3350 |
| 3250 | — | — | — | — | 3250 | 3250 | 3250 | — | 3250 | 3250 | 3250 | — | — | — |
| 3150 | 3150 | 3150 | 3150 | 3150 | 3150 | 3150 | 3150 | 3150 | 3150 | 3150 | 3150 | 3150 | — | — |
| 3000 | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 2300 | 2300 | 2300 | 2300 | 2300 | 2300 | 2300 | — | — | — | — | 2300 | — | — | — |
| — | — | — | — | 2000 | 2000 | — | — | — | 2000 | — | — | — | 2000 | 2000 |
| — | — | 1825 | — | — | — | — | — | — | — | — | — | — | — | — |
| 1750 | 1750 | 1750 | 1750 | — | — | 1750 | 1750 | 1750 | — | 1750 | — | 1750 | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1675 |
| — | — | — | — | — | — | — | — | — | — | — | — | 1625 | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | 1600 | — | — |
| — | — | 1475 | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — | 1450 | 1450 |
| — | — | — | — | — | — | — | 1400 | 1400 | 1400 | — | — | 1400 | — | — |
| — | — | — | — | — | — | — | — | — | — | — | 1350 | — | — | — |
| 1250 | 1250 | 1250 | 1250 | 1250 | 1250 | 1250 | 1250 | 1250 | 1250 | — | 1250 | 1250 | — | — |
| — | — | — | — | — | — | — | 900 | 900 | 900 | — | — | 900 | — | — |
| 860 | — | 860 | 860 | 860 | 860 | 860 | 860 | 860 | 860 | 860 | 860 | 860 | 860 | 860 |
| — | 600 | — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | 400 | — | — | — |
| 320 | — | — | — | — | 320 | 320 | 320 | — | 320 | 320 | 320 | 320 | — | — |
| 300 | 300 | NV | 300 | — | — | 300 | 300 | 300 | — | 300 | 300 | 300 | — | — |
| — | NV | — | — | — | — | — | — | — | — | — | — | — | — | — |
| NV | NV | NV | 250 | NV | NV | 250 | NV | NV | NV | NV | NV | NV | NV | NV |
| 16,180 | 16,250 | 16,160 | 16,510 | 16,460 | 16,480 | 16,530 | 16,530 | 16,510 | 16,480 | 16,430 | 16,530 | 16,505 | 16,510 | 16,535 |

*Hind* III

| A | B | C | D | E | F |
|---|---|---|---|---|---|
| 6950 | 6950 | — | — | — | — |
| — | — | 6150 | 6150 | — | 6150 |
| — | — | — | — | 6000 | — |
| 4200 | — | — | — | — | 4200 |
| — | 2300 | 2300 | 2300 | 2300 | — |
| 2200 | 2200 | 2200 | 2200 | 2200 | 2200 |
| — | 2000 | 2000 | — | 2000 | — |
| 1800 | 1800 | 1800 | 1800 | 1800 | 1800 |
| 1550 | 1550 | 1550 | 1550 | 1550 | 1550 |
| — | — | — | 1000 | — | — |
| — | — | 980 | 980 | 980 | 980 |
| — | — | — | 925 | — | — |
| 440 | 440 | 440 | 440 | 440 | 440 |
| — | — | — | — | NV | — |
| 17,140 | 17,240 | 17,420 | 17,345 | 17,270 | 17,320 |

*Nde* I

| A | B | C | D |
|---|---|---|---|
| — | 7200 | — | — |
| 6100 | — | — | — |
| — | 3700 | 3700 | 3700 |
| 3650 | — | 3650 | 3650 |
| 3600 | — | 3600 | 3600 |
| 3100 | 3100 | 3100 | — |
| — | — | — | 2650 |
| — | 2400 | 2400 | 2400 |
| — | — | — | 425 |
| 16,450 | 16,400 | 16,450 | 16,425 |

*Pst* I

| A | B | C | D |
|---|---|---|---|
| BYSUB | — | — | — |
| — | BYSUB | — | — |
| — | — | BYSUB | — |
| — | — | — | BYSUB |
| — | — | — | 3100 |
| — | 1100 | 1100 | 1100 |
| — | — | NV | NV? |

*Nco* I

| B | C | D | E | F |
|---|---|---|---|---|
| NOSITE | — | — | — | — |
| — | BYSUB | — | — | — |
| — | — | — | BYSUB | — |
| — | — | — | — | BYSUB |
| — | — | BYSUB | — | — |
| — | — | 2900 | — | — |
| — | — | — | — | 950 |

*Pvu* II

| B | C | D | E | F |
|---|---|---|---|---|
| BYSUB | — | — | — | — |
| — | 8800 | — | 8800 | — |
| 6000 | 6000 | 6000 | — | — |
| — | — | 4600 | — | 4600 |
| — | — | 3700 | — | 3700 |
| — | — | — | 3080 | 3080 |
| — | — | — | 2950 | 2950 |
| — | 2200 | 2200 | 2200 | 2200 |
| | 17,000 | 16,500 | 17,030 | 16,530 |

*Sac* I

| B | C | D |
|---|---|---|
| BYSUB | — | — |
| — | 9000 | — |
| — | 7900 | 7900 |
| — | — | 4400 |
| — | — | 4100 |
| | 16,900 | 16,400 |

*Stu* I

| Y | Z | A | B | C | D | F | G | H | I |
|---|---|---|---|---|---|---|---|---|---|
| 4000 | — | — | — | — | — | 4000 | 4000 | 4000 | 4000 |
| — | — | — | 3700 | — | — | — | — | 3700 | — |
| — | — | — | — | 3200 | — | — | — | — | — |
| 2900 | 2900 | 2900 | 2900 | 2900 | 2900 | 2900 | 2900 | 2900 | 2900 |
| — | 2600 | 2600 | 2600 | 2600 | 2600 | — | — | — | — |
| 2350 | 2350 | 2350 | 2350 | 2350 | 2350 | 2350 | 2350 | 2350 | 2350 |
| 2100 | 2100 | 2100 | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | 1900 |
| — | — | — | — | — | 1750 | — | — | — | — |
| — | — | — | — | — | — | 1700 | — | — | 1700 |
| 1600 | 1600 | 1600 | — | — | — | — | — | — | — |
| — | — | — | — | — | — | 1500 | 1500 | — | — |
| 1450 | 1450 | — | — | — | 1450 | — | — | — | — |
| — | — | — | — | — | — | — | 1425 | — | — |
| — | 1420 | 1420 | 1420 | 1420 | 1420 | — | — | — | — |
| 1250 | 1250 | 1250 | 1250 | 1250 | 1250 | 1250 | 1250 | 1250 | 1250 |
| — | — | 1030 | 1030 | 1030 | 1030 | 1030 | 1030 | 1030 | 1030 |
| 560 | 560 | 560 | 560 | 560 | 560 | 560 | 560 | 560 | 560 |
| — | — | — | — | 500 | 500 | 500 | 500 | — | — |
| — | — | 420 | 420 | 420 | 420 | 420 | 420 | 420 | 420 |
| — | — | — | — | — | — | — | 350 | — | NV |
| NV | NV | 220 | NV | NV | NV | NV | NV | 220 | NV |
| NV | NV | 155 | NV | NV | NV | NV | NV | 155 | NV |
| 16,210 | 16,230 | 16,605 | 16,230 | 16,230 | 16,230 | 16,210 | 16,285 | 16,585 | 16,110 |

Matrix of presence (1) and absence (0) of 108 restriction sites in 58 *Coereba flaveola* mitochondrial DNA haplotypes. Haplotype acronyms are from table 2. Sites are presented by restriction enzymes: *Bam*H I, *Bgl* I, *Bgl* II, *Cla* I, *Dra* I, *Eco*R I, *Eco*R V, *Hin*d III, *Nco* I, *Nde* I, *Pst* I, *Pvu* II, *Sac* I, *Stu* I, *Ava* I, and *Hin*c II.

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| JA1 | 11100 | 1110000 | 1100 | 110 | 111000 | 111000 | 110000 | 1111110010 | 100 | 111100 | 1111 |
| | 11101 | 110 | 11111111110000 | 11111110 | 10011110000000011 | | | | | | |
| JA2 | 11100 | 1110000 | 1100 | 110 | 111000 | 111010 | 110001 | 1111110010 | 100 | 111100 | 1111 |
| | 11101 | 110 | 11111111100000 | 11111110 | 10011110000000011 | | | | | | |
| JA3 | 11100 | 1110000 | 1100 | 110 | 111000 | 111010 | 110001 | 1111110010 | 100 | 111100 | 1111 |
| | 11101 | 110 | 11110111000000 | 11111110 | 10011100000010011 | | | | | | |
| JA4 | 11100 | 1110000 | 1100 | 111 | 111000 | 111010 | 110001 | 1111110010 | 100 | 111100 | 1111 |
| | 11101 | 110 | 11111111100000 | 11111110 | 10011100000010011 | | | | | | |
| JA5 | 11100 | 1110000 | 1100 | 111 | 111000 | 111011 | 110001 | 1111110010 | 100 | 111100 | 1111 |
| | 11101 | 110 | 11111111100000 | 11111110 | 10011100000010011 | | | | | | |
| JA6 | 11100 | 1110000 | 1100 | 100 | 111000 | 111010 | 110001 | 1111100010 | 100 | 111100 | 1111 |
| | 11101 | 110 | 11111111100000 | 11111100 | 10011100000010011 | | | | | | |
| PR1 | 10010 | 1110000 | 1110 | 100 | 111000 | 111000 | 111100 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110110000 | 11111100 | 11111111010000010 | | | | | | |
| PR2 | 10010 | 1110000 | 1110 | 100 | 111000 | 111000 | 111100 | 1111111110 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110110000 | 11111100 | 11111110010000010 | | | | | | |
| PR3 | 10010 | 1110000 | 1110 | 100 | 111000 | 111100 | 111100 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110110000 | 11111100 | 11111110100000010 | | | | | | |
| PR4 | 10010 | 1110000 | 1110 | 100 | 111000 | 111100 | 111100 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110110000 | 11111100 | 11111110110000010 | | | | | | |
| PR5 | 10010 | 1110000 | 1110 | 100 | 111000 | 111100 | 111100 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110110000 | 11111100 | 11111100110000010 | | | | | | |
| PR6 | 10010 | 1110000 | 1110 | 100 | 111000 | 111100 | 111100 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110110000 | 11111100 | 11111110110100010 | | | | | | |
| PR7 | 10010 | 1110000 | 1110 | 100 | 111000 | 111100 | 111100 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110110000 | 11111000 | 11111110110000010 | | | | | | |
| PR8 | 10010 | 1110000 | 1110 | 100 | 111000 | 111100 | 111100 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111111110000 | 11111100 | 11111110110000010 | | | | | | |
| PR9 | 10010 | 1110000 | 1110 | 100 | 111000 | 111100 | 111100 | 1111111010 | 100 | 110110 | 1110 |
| | 11100 | 110 | 11111111110000 | 11111100 | 11111110110000010 | | | | | | |
| PR10 | 10010 | 1110000 | 1110 | 100 | 111000 | 111100 | 111100 | 1111111010 | 100 | 111110 | 1110 |
| | 11101 | 110 | 11111111110000 | 11111100 | 11111110110000010 | | | | | | |
| PR11 | 10010 | 1110000 | 1110 | 100 | 111000 | 111100 | 110100 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111111110000 | 11111100 | 11111110110000010 | | | | | | |
| PR12 | 10010 | 1110000 | 1110 | 100 | 111010 | 111100 | 111100 | 1111111010 | 100 | 111110 | 1110 |
| | 11101 | 110 | 11111111110000 | 11111100 | 11111110100000010 | | | | | | |
| LA1 | 10010 | 1111000 | 1100 | 100 | 111000 | 111000 | 110000 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110111000 | 11111100 | 11111110100000010 | | | | | | |
| LA2 | 10100 | 1111000 | 1100 | 100 | 111000 | 111000 | 110000 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110111000 | 11111100 | 11111110100000010 | | | | | | |
| LA3 | 10100 | 1111000 | 1100 | 100 | 111100 | 111000 | 110000 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110111000 | 11111100 | 11111110100000010 | | | | | | |
| LA4 | 10010 | 1111000 | 1100 | 100 | 111100 | 111000 | 110000 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110111000 | 11111100 | 11111110100000010 | | | | | | |
| LA5 | 10010 | 1111000 | 1100 | 100 | 111001 | 111000 | 110000 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110111000 | 11111100 | 11111110100000010 | | | | | | |
| LA6 | 10010 | 1111100 | 1100 | 100 | 111000 | 111000 | 110000 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110111000 | 11111100 | 11111110100000010 | | | | | | |
| LA7 | 10010 | 1111100 | 1100 | 100 | 111000 | 111000 | 110001 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110111000 | 11111100 | 11111110100000010 | | | | | | |
| LA8 | 10010 | 1111100 | 1100 | 100 | 111000 | 111000 | 110001 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110111000 | 11111100 | 11111110100000110 | | | | | | |
| LA9 | 10010 | 1111000 | 1100 | 100 | 111000 | 111000 | 110001 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110111000 | 11111100 | 11111110100000010 | | | | | | |
| LA10 | 10010 | 1111100 | 1100 | 100 | 111000 | 111100 | 110001 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110111000 | 11111100 | 11111110100000010 | | | | | | |
| LA11 | 10010 | 1111000 | 1100 | 100 | 111000 | 111000 | 110000 | 1111111011 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110111000 | 11111100 | 11111110100000010 | | | | | | |
| LA12 | 10010 | 1111000 | 1100 | 100 | 111000 | 111000 | 110000 | 1111111010 | 000 | 111110 | 1110 |
| | 11100 | 110 | 11111110111000 | 11111100 | 11111110100000010 | | | | | | |
| LA13 | 10010 | 1111000 | 1100 | 100 | 111000 | 111000 | 110000 | 1111111010 | 100 | 111111 | 1110 |
| | 11100 | 110 | 11111110111000 | 11111100 | 11111110100000010 | | | | | | |
| LA14 | 10010 | 1111000 | 1100 | 100 | 111000 | 111000 | 110000 | 1111111010 | 100 | 111110 | 1110 |
| | 11000 | 110 | 11111110111000 | 11111100 | 11111110100000010 | | | | | | |
| LA15 | 10010 | 1111000 | 1100 | 100 | 111000 | 111000 | 110000 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 100 | 11111110111000 | 11111100 | 11111110100000010 | | | | | | |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| LA16 | 10010 | 1111000 | 1100 | 100 | 111000 | 111000 | 110000 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110111100 | 11111100 | 111111110100000010 | | | | | | |
| LA17 | 10010 | 1111000 | 1100 | 100 | 111000 | 111000 | 110000 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110111000 | 11111100 | 110111110100000010 | | | | | | |
| LA18 | 10010 | 1111000 | 1100 | 100 | 111000 | 111000 | 110000 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110111000 | 11111100 | 111111110101000010 | | | | | | |
| LA19 | 10010 | 1111010 | 1100 | 100 | 111010 | 111000 | 110000 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110111000 | 11111100 | 111111110100000010 | | | | | | |
| GSV1 | 10010 | 1110000 | 1100 | 100 | 111000 | 111000 | 111000 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110110000 | 11111100 | 111111110100000010 | | | | | | |
| GSV2 | 10010 | 1110000 | 1100 | 100 | 111000 | 111000 | 111000 | 1111111010 | 100 | 111110 | 1110 |
| | 11100 | 110 | 11111110110000 | 11111100 | 111111110000000010 | | | | | | |
| GSV3 | 10010 | 1110000 | 1100 | 100 | 111000 | 111000 | 111000 | 1111111010 | 100 | 111110 | 1110 |
| | 11110 | 110 | 11111110110000 | 11111100 | 111111110100000010 | | | | | | |
| GSV4 | 10010 | 1110000 | 1100 | 100 | 111000 | 111000 | 111000 | 1111111010 | 100 | 111110 | 1110 |
| | 11110 | 110 | 11111110110000 | 11111100 | 111111110100000010 | | | | | | |
| GSV5 | 10010 | 1110000 | 1100 | 100 | 111000 | 111000 | 111000 | 1111111010 | 100 | 111110 | 1110 |
| | 11110 | 110 | 11111110110000 | 11111100 | 111111100100000010 | | | | | | |
| GSV6 | 10010 | 1110000 | 1100 | 100 | 111000 | 111000 | 111000 | 1111111010 | 100 | 111110 | 1110 |
| | 11110 | 111 | 11111110110000 | 11111100 | 111111110100000010 | | | | | | |
| GSV7 | 10010 | 1110000 | 1100 | 100 | 111000 | 111000 | 110000 | 1111111010 | 100 | 111110 | 1110 |
| | 11110 | 111 | 11111110110000 | 11111100 | 111111110100000010 | | | | | | |
| GSV8 | 10010 | 1110000 | 1100 | 100 | 111000 | 111000 | 111000 | 1111111010 | 100 | 111110 | 1110 |
| | 11111 | 110 | 11111110110000 | 11111100 | 111111110100000010 | | | | | | |
| VE1 | 10010 | 1111000 | 1100 | 100 | 111000 | 111000 | 110010 | 1111111010 | 110 | 111110 | 1100 |
| | 11100 | 110 | 11111010110000 | 11111110 | 111111110000000010 | | | | | | |
| VE2 | 10010 | 1111000 | 1100 | 100 | 111000 | 111000 | 110110 | 1111111010 | 110 | 111110 | 1100 |
| | 11100 | 110 | 11111010110010 | 11111110 | 111111110000000010 | | | | | | |
| VE3 | 10100 | 1111000 | 1100 | 100 | 111000 | 111000 | 110110 | 1111111010 | 110 | 111110 | 1100 |
| | 11100 | 110 | 11111010110000 | 11111110 | 111111110000000010 | | | | | | |
| VE4 | 10010 | 1111000 | 1100 | 100 | 111000 | 111000 | 110110 | 1111111010 | 110 | 111110 | 1100 |
| | 11100 | 110 | 11111010110000 | 11111110 | 111111110000000010 | | | | | | |
| VE5 | 10011 | 1111000 | 1100 | 100 | 111000 | 111000 | 110110 | 1111101010 | 011 | 111110 | 1100 |
| | 11100 | 110 | 11111010110000 | 11111110 | 111111110000000010 | | | | | | |
| VE6 | 10010 | 1111000 | 1100 | 100 | 111000 | 111000 | 110110 | 1111101010 | 010 | 111110 | 1100 |
| | 11100 | 110 | 11111010110000 | 11111110 | 111111110000000010 | | | | | | |
| VE7 | 10010 | 1111000 | 1100 | 100 | 111000 | 111000 | 110110 | 1111111010 | 010 | 111110 | 1000 |
| | 11100 | 110 | 11111010110000 | 11111110 | 111111110000000010 | | | | | | |
| VE8 | 10010 | 1111001 | 1100 | 100 | 111000 | 111000 | 110110 | 1111111010 | 010 | 111110 | 1000 |
| | 11100 | 110 | 11111010110000 | 11111110 | 111111110000000010 | | | | | | |
| CA1 | 10100 | 1110000 | 1101 | 100 | 111000 | 111000 | 110010 | 1111111010 | 100 | 111110 | 1100 |
| | 11100 | 110 | 11111010111011 | 11111110 | 111111111000000010 | | | | | | |
| CA2 | 10100 | 1110000 | 1101 | 100 | 111000 | 111000 | 110010 | 1111111010 | 100 | 111110 | 1100 |
| | 11100 | 110 | 11111010111010 | 11111110 | 111111111000000010 | | | | | | |
| CA3 | 10100 | 1110000 | 1101 | 100 | 111000 | 111000 | 110010 | 1111111010 | 100 | 111110 | 1100 |
| | 11110 | 110 | 11111010111010 | 11111110 | 111111111000000010 | | | | | | |
| CA4 | 10100 | 1110000 | 1101 | 100 | 111000 | 111000 | 110010 | 1111111010 | 100 | 111110 | 1100 |
| | 11100 | 110 | 11111010111010 | 11111100 | 111111100000000010 | | | | | | |
| CA5 | 10010 | 1110100 | 1101 | 100 | 111000 | 111000 | 110010 | 1111111010 | 100 | 111110 | 1100 |
| | 11100 | 110 | 11111010111010 | 11111111 | 111111110000000010 | | | | | | |