# GENIC VARIABILITY AND DIFFERENTIATION IN THE GALAPAGOS FINCHES

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ABSTRACT.—Electrophoretic methods were used to examine patterns of genic variation within and between populations of 11 species of Galapagos finches (Geospizinae) and to examine phyletic relationships among these species. Levels of genetic heterozygosity are moderate and are similar to those found for other vertebrates, including birds. Interpopulation levels of genic differentiation are slight for all species except the Warbler Finch (*Certhidea olivacea*), which exhibits marked differentiation. Nevertheless, the island populations of finch species are several times more differentiated than are populations of mainland avian species. The patterns of both within and between population genic variation are most easily explained as functions of population size and the degree of interisland movements. The relationships among the finch taxa suggested by the biochemical data are quite concordant with the traditional view based on morphology. *Received 7 August 1980, accepted 29 September 1980.*

BEGINNING with the observations of Charles Darwin (1859) and supported subsequently by the detailed studies of Lack (1945, 1947), the Galapagos finches (Geospizinae) have become a textbook example of adaptive radiation. The radiation has been studied extensively from morphological, distributional, and ecological viewpoints (Lack 1947; Bowman 1961, 1963; Abbott et al. 1977), and one analysis of blood protein variation is available (Ford et al. 1974). We report here on an analysis of genic levels of differentiation accompanying the radiation, as measured by electromorphic (= allozyme) variation patterns within and between the species of Galapagos finches.

## MATERIALS AND METHODS

A total of 250 specimens of geospizines, including representatives of 51 populations and 11 of the 13 currently recognized species, was available for study. Only the Mangrove Finch (*Cactospiza heliobates*) and one of the insectivorous tree-finches (*Camarhynchus psittacula*) were unavailable for study. Sampling efficiency across the taxa represented and the islands they inhabit varied widely (Table 1). All individuals were collected using mist nets during January and February 1974. Tissues (kidney, liver, heart, and muscle) were removed and maintained on liquid nitrogen (−196°C) until transported to the laboratory, where subsequent maintenance was at −76°C.

Twenty-seven presumptive genetic loci were examined by horizontal starch gel electrophoresis using standard procedures (see Selander et al. 1971, Ayala et al. 1972) as follows: Lithium Hydroxide (Buffer #2 of Selander et al. 1971; 300 volts, 3 h)—leucine amino peptidase (LAP), general proteins [albumin (Alb) and protein-1 (Pt-1)], and esterases (Est-1, Est-2, and Est-3); Poulik (buffer #3 of Selander et al. 1971; 200 volts, 3 h)—lactate dehydrogenase (LDH-1 and LDH-2) and peptidase (Pept-1 and Pept-2); Tris Maleate (buffer #9 of Selander et al. 1971; 100 volts, 4 h)—6 phosphogluconate dehydrogenase (6PGD); Tris Citrate II (buffer #5 of Selander et al. 1971; 100 volts, 4 h)—α glycerophosphate dehydrogenase (αGPD-1 and αGPD-2), malate dehydrogenase (MDH-1 and MDH-2), and glutamate-oxaloacetate transaminase (GOT-1 and GOT-2); Tris-versene-borate (buffer #6 of Selander et al. 1971; 200 volts, 3 h)—alcohol dehydrogenase (ADH) and superoxide dismutase (SOD+ and SOD−; observed on the ADH stain); Phosphate buffer (buffer #7 of Selander et al. 1971; 130 volts, 3.5 h)—phosphogluconate isomerase (PGI), phosphoglucomutase (PGM-1 and PGM-2), mannose phosphate isomerase (MPI); Phosphate-Citrate

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TABLE 1. Efficiency of sampling program of 11 taxa of finches in the Galápagos Archipelago.

| Taxon | Number of islands inhabited | Number of islands sampled (percentage of islands sampled) | $n_{Total}$ | $\bar{n}_{Island}$ |
|---|---|---|---|---|
| Large Ground-Finch (*Geospiza magnirostris*) | 12 | 4 (33) | 17 | 4.3 |
| Medium Ground-Finch (*G. fortis*) | 12 | 8 (67) | 53 | 6.6 |
| Small Ground-Finch (*G. fuliginosa*) | 12 | 10 (83) | 80 | 8.0 |
| Sharp-beaked Ground-Finch (*G. difficilis*) | 9 | 3 (33) | 5 | 1.7 |
| Cactus Ground-Finch (*G. scandens*) | 10 | 3 (30) | 26 | 8.7 |
| Large Cactus Ground-Finch (*G. conirostris*) | 4 | 2 (50) | 21 | 10.5 |
| Vegetarian Tree-Finch (*Platyspiza crassirostris*) | 9 | 4 (44) | 8 | 2.0 |
| Medium Insectivorous Tree-Finch (*Camarhynchus pauper*) | 1 | 1 (100) | 3 | 3.0 |
| Small Insectivorus Tree-Finch (*C. parvulus*) | 10 | 4 (40) | 21 | 5.3 |
| Woodpecker Finch (*Cactospiza pallida*) | 7 | 1 (14) | 1 | 1.0 |
| Warbler Finch (*Certhidea olivacea*) | 15 | 4 (27) | 15 | 3.8 |

buffer (buffer #8 of Selander et al. 1971; 100 volts, 4 h)—isocitrate dehydrogenase (IDH-1 and IDH-2) and sorbitol dehydrogenase (SDH). Albumin is the most anodally migrating protein and protein-1 is the only cathodal protein on LiOH gels; Est-1 and Est-2 are anodal proteins, and Est-3 is a cathodal protein using $\alpha$NP + FBRR. A leucyl-glycyl substrate was used for peptidase activity on Poulik gels. A single homogenate combining kidney, liver, and heart was used for all protein assays.

Alleles (= electromorphs) at each locus were designated alphabetically in decreasing order of mobility. In the case of multiple isozymes for a given protein, the most anodal locus was designated "1," with more cathodal loci indicated by progressively higher numbers.

Heterozygosity levels were determined by direct count. Allelic frequencies were converted to genetic distances using the methods of Rogers (1972) and Nei (1972), as corrected for small sample size (Nei and Roychoudhury 1974, Nei 1978). Patterns of population or species relatedness were examined by average linkage phenetic clustering techniques (UPGMA; Sneath and Sokal 1973) and by the construction of phylogenetic trees, using a matrix of Rogers' *D*-values, following the methods of Fitch and Margoliash (1967) and Farris (1972). Wright's (1965) $F_{ST}$, an inbreeding coefficient, was computed with the modifications of Nei (1965) for multiple alleles and Wright (1978) for small sample size.

## RESULTS AND DISCUSSION

Because of the restricted sample sizes, the population data matrix has been reduced so that allele frequencies are presented only at the species level in Table 2. Of the 27 loci examined, 11 are polymorphic across the taxa studied, 8 are weakly polymorphic (minor alleles generally less than 5% in frequency), and 8 are monomorphic and fixed for the same allele in all taxa.

*Within population variation.*—Species heterozygosity levels are presented in Table 3. Averaging population samples for at least seven species provides data sufficient for heterozygosity determinations based on the criteria of Nei and Roychoudhury (1974) and comparable to those for other organisms. For most taxa, heterozygosities are moderate (average of 4–5% across all taxa) and well within the range reported for other birds (Barrowclough and Corbin 1978, Avise et al. 1980) and for vertebrates in general (Selander and Johnson 1973, Nevo 1978). Excepting the Large Ground-Finch (*G. magnirostris*), the species of *Geospiza* have uniformly high heterozygosities; all other taxa possess intermediate levels save the Cactus Finch (*Cactospiza pallida*), which lacks variability based on the single individual examined. The relatively high within-species variability levels are somewhat surprising, as most island species characteristically exhibit lowered variability in comparison to mainland relatives (Selander 1976). If the measures of heterozygosity for passerine

TABLE 2. Allele frequencies pooled across all sampled populations for 11 species of Galapagos finches. All taxa are monomorphic and fixed for the same allele at 8 loci (αGPD-1, 6PGD, LAP, Pept-2, IPO+, IPO−, MDH-1, and Alb).

| Locus | Allele | *Geospiza fortis* | *G. scandens* | *G. fuliginosa* | *G. difficilis* | *G. magnirostris* | *G. conirostris* | *Camarhynchus pauper* | *C. parvulus* | *Certhidea olivacea* | *Cactospiza pallida* | *Platyspiza crassirostris* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| IDH-1 | a | 0.010 | | | | | | | | | | |
| | b | 0.679 | 0.288 | 0.581 | 0.900 | 0.765 | 0.929 | | 0.048 | | | 0.063 |
| | c | 0.311 | 0.712 | 0.419 | 0.100 | 0.235 | 0.071 | 1.00 | 0.952 | 1.00 | 1.00 | 0.937 |
| IDH-2 | a | | | 0.006 | | | | | | | | |
| | b | 1.00 | 1.00 | 0.982 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |
| | c | | | 0.006 | | | | | | | | |
| | d | | | 0.006 | | | | | | | | |
| ADH | a | 1.00 | 0.942 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |
| | b | | 0.058 | | | | | | | | | |
| αGPD-2 | a | | | 0.006 | | | | | | | | |
| | b | 1.00 | 1.00 | 0.994 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.967 | 1.00 | 1.00 |
| | c | | | | | | | | | 0.033 | | |
| SDH | a | 0.009 | | | | | | | | | | |
| | b | 0.642 | 0.981 | 0.356 | 0.600 | 0.029 | 0.071 | | 0.190 | 0.067 | | |
| | c | 0.349 | | 0.644 | 0.400 | 0.971 | 0.929 | 1.00 | 0.810 | 0.933 | 1.00 | 1.00 |
| | d | | 0.019 | | | | | | | | | |
| GOT -1 | a | | | | | | | | | 0.767 | | |
| | b | 0.018 | | 0.006 | 0.100 | | | | | | | |
| | c | 0.973 | 1.00 | 0.994 | 0.900 | 1.00 | 1.00 | 1.00 | 1.00 | 0.233 | 1.00 | 1.00 |
| | d | 0.009 | | | | | | | | | | |
| GOT-2 | a | | 0.019 | | 0.100 | | 0.167 | | | | | |
| | b | 1.00 | 0.981 | 1.00 | 0.900 | 1.00 | 0.833 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |
| MDH-2 | a | 0.991 | 0.962 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |
| | b | 0.009 | | | | | | | | | | |
| | c | | 0.038 | | | | | | | | | |
| PGI | a | 0.028 | | 0.025 | | | 0.024 | | 0.033 | | | |
| | b | 0.953 | 1.00 | 0.969 | 1.00 | 1.00 | 0.976 | 0.833 | 0.967 | 1.00 | 1.00 | 0.937 |
| | c | | | | | | | 0.167 | | | | |
| | d | 0.019 | | 0.006 | | | | | | | | 0.063 |
| PGM-2 | a | 0.009 | | | | | | | | | | |
| | b | 0.075 | 0.135 | 0.056 | | 0.118 | 0.024 | | 0.071 | 0.033 | | |
| | c | | 0.019 | 0.013 | 0.100 | 0.029 | | | | | | |
| | d | 0.898 | 0.846 | 0.931 | 0.900 | 0.853 | 0.976 | 1.00 | 0.929 | 0.400 | 1.00 | 1.00 |
| | e | | | | | | | | | 0.567 | | |
| | f | 0.009 | | | | | | | | | | |
| | g | 0.009 | | | | | | | | | | |

TABLE 2. Continued.

| Locus | Allele | *Geospiza fortis* | *G. scandens* | *G. fuliginosa* | *G. difficilis* | *G. magnirostris* | *G. conirostris* | *Camarhynchus pauper* | *C. parvulus* | *Certhidea olivacea* | *Cactospiza pallida* | *Platyspiza crassirostris* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PGM-1 | a | 0.009 | | 0.006 | 0.100 | | | | | 0.033 | | |
| | b | 0.057 | 0.019 | 0.094 | 0.200 | 0.029 | 0.500 | 0.833 | 0.905 | 0.233 | 1.00 | 0.438 |
| | c | 0.009 | | 0.019 | | | | | | | | |
| | d | 0.916 | 0.981 | 0.881 | 0.700 | 0.971 | 0.500 | 0.167 | 0.095 | 0.734 | | 0.499 |
| | e | | | | | | | | | | | 0.063 |
| | f | 0.009 | | | | | | | | | | |
| LDH-1 | a | | | | | | | | 0.024 | | | |
| | b | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.976 | 1.00 | 1.00 | 1.00 |
| LDH-2 | a | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.967 | 1.00 | 1.00 |
| | b | | | | | | | | | 0.033 | | |
| Pept-1 | a | | 0.038 | 0.019 | | | | | | | | |
| | b | 0.991 | 0.924 | 0.962 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |
| | c | 0.009 | 0.038 | 0.019 | | | | | | | | |
| MPI | a | 0.038 | 0.096 | 0.044 | | 0.029 | 0.310 | | | | | |
| | b | 0.887 | 0.635 | 0.818 | 0.900 | 0.912 | 0.452 | 1.00 | 0.952 | 1.00 | 1.00 | 0.812 |
| | c | | | 0.019 | | | | | | | | |
| | d | 0.066 | 0.269 | 0.119 | 0.100 | 0.059 | 0.238 | | 0.048 | | | 0.188 |
| | e | 0.009 | | | | | | | | | | |
| Pt-1 | a | 0.028 | 0.038 | | 0.100 | 0.059 | | | | | | |
| | b | 0.972 | 0.962 | 1.00 | 0.900 | 0.941 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |
| Est-1 | a | | | | | | | | | 0.300 | | |
| | b | 0.047 | | 0.006 | 0.100 | 0.059 | | | | 0.700 | | |
| | c | | | | | | | | | | 1.00 | 1.00 |
| | d | 0.953 | 1.00 | 0.994 | 0.900 | 0.941 | 1.00 | 1.00 | 1.00 | | | |
| Est-2 | a | | 0.038 | | | | | | | | | |
| | b | 1.00 | 0.962 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |
| Est-3 | a | 0.991 | 1.00 | 0.982 | 1.00 | 1.00 | 1.00 | 1.00 | 0.905 | 0.367 | 1.00 | 1.00 |
| | b | | | 0.006 | | | | | | | | |
| | c | 0.009 | | | | | | | | | | |
| | d | | | 0.012 | | | | | | | | |
| | e | | | | | | | | 0.095 | 0.633 | | |

TABLE 3. Weighted and unweighted mean heterozygosity ($\bar{H}$) levels for 11 species of Galapagos finches.

| Taxon | $n_{sample}$ | $\bar{H}_{weighted}$ | $\bar{H}_{unweighted}$ |
|---|---|---|---|
| *Geospiza* | | | |
| *fortis* | 53 | 0.0566 | 0.0522 |
| *scandens* | 26 | 0.0579 | 0.0628 |
| *fuliginosa* | 80 | 0.0620 | 0.0649 |
| *difficilis* | 5 | 0.0815 | 0.0679 |
| *magnirostris* | 17 | 0.0349 | 0.0288 |
| *conirostris* | 21 | 0.0564 | 0.0561 |
| | $\bar{H}$ | 0.0576 | 0.0528 |
| *Camarhynchus* | | | |
| *pauper* | 3 | 0.0247 | |
| *parvulus* | 21 | 0.0300 | 0.0337 |
| *Cactospiza pallida* | 1 | 0.0000 | |
| *Platyspiza crassirostris* | 8 | 0.0370 | 0.0440 |
| *Certhidea olivacea* | 15 | 0.0272 | 0.0278 |
| | $\bar{H}_{over\ all\ taxa}$ | 0.0522 | 0.0426 |

species available to date continue to be representative of birds, the values for Galapagos finches suggest that (1) a severe population bottleneck at species founding was not experienced, and/or (2) large population levels were quickly regained subsequent to founding. Both the extent of bottlenecking and the rate of population recovery are related to expected heterozygosity levels (Nei et al. 1975). A third possible explanation is that population bottlenecks occurred long ago; the effects of a bottleneck become undetectable after $10^5$–$10^6$ yr (Nei et al. 1975). Most finch species probably had their origins more recently, however (see below), and it is likely that many island populations have experienced repeated fluctuations in density since their founding.

As heterozygosity levels are not directly related to sample size ($r = 0.447$; $P > 0.25$), some suggestive statements regarding patterns of within-species population variability can be made. In general, $\bar{H}$ is either uniform or haphazardly varying across islands for those species from which four or more populations have been examined (Table 4). There is no apparent relationship between $\bar{H}$ and finch community structure (i.e. number of sympatric congeners or consubfamilial species; $r < 0.55$ with $P > 0.25$ in all comparisons) or species within-population morphological variability measures of bill depth or culmen length ($r < -0.32$ with $P > 0.25$ in all cases; data from Bowman 1961: Table 61). The only decidedly nonrandom pattern found is in the Warbler Finch (*Certhidea olivacea*); here, $\bar{H}$ is positively and significantly ($P < 0.05$) correlated with island size (Table 4), which is a measure of both ecological amplitude (Bowman 1961, Preston 1962a, Hamilton and Rubinoff 1963, Abbott et al. 1977) and probably total population size.

While the possibility of a direct genetic-environmental relationship in *Certhidea* may be appealing, heterozygosity patterns in this and other Galapagos finches are more likely a reflection of population size (including absolute numbers and the degree to which island populations are connected by movements). This is suggested by at least four features: (1) There is a lack of correlation within the *Geospiza* and *Camarhynchus* species examined with island size (Table 4) or, indeed, with measures of more direct ecological diversity, such as the number of plant species or genera per island ($r < 0.03$ in all cases; data from Preston 1962a, Wiggins and Porter 1971,

TABLE 4. Population mean heterozygosity ($\bar{H}$) values for those species of Galapagos finches for which at least four island populations were sampled. Sample sizes in parentheses.

| Island | Log area | *Geospiza magniro-stris* | *G. fuliginosa* | *G. fortis* | *Cama-rhynchus parvulus* | *Certhidea olivacea* |
|---|---|---|---|---|---|---|
| Isabela | 3.352 | | 0.0635 (7) | 0.0617 (6) | | |
| Santa Cruz | 2.995 | | 0.0509 (8) | 0.0456 (13) | 0.0159 (7) | 0.0556 (4) |
| Fernandina | 2.389 | | 0.0741 (1) | | | |
| Santiago | 2.308 | 0.0296 (5) | 0.0617 (15) | 0.0611 (21) | 0.0296 (10) | |
| San Cristobal | 2.290 | | 0.0593 (10) | | 0.0741 (2) | |
| Floreana | 1.806 | | 0.0741 (9) | 0.0556 (4) | 0.0370 (2) | |
| Marchena | 1.653 | 0.0278 (4) | 0.0741 (4) | 0.0750 (3) | | 0.0370 (1) |
| Pinta | 1.301 | 0.0423 (7) | 0.0337 (11) | 0.0875 (3) | | |
| Espanola | 1.255 | | 0.0535 (9) | | | 0.0185 (8) |
| Santa Fe | 0.875 | | 0.0556 (6) | 0.0370 (2) | | |
| Genovesa | 0.643 | 0.0370 (1) | | 0.0370 (1) | | 0.0000 (2) |
| | $r$ = | 0.622 | 0.244 | 0.160 | 0.425 | 0.966 |
| | $P$ | $> 0.10$ | $> 0.25$ | $> 0.25$ | $> 0.25$ | $< 0.05$ |

Abbott et al. 1977). (2) There is a relationship between $\bar{H}$ and taxonomic diversity within the species in question. Over the islands sampled, all three *Geospiza* species, while exhibiting some variation in quantitative characters, do not show overall morphological differentiation of a form that has been considered suitable for subspecific recognition, whereas each of the populations of *Certhidea* examined belongs to separate races (Lack 1945, 1947). This suggests either that the *Geospiza* species are more recent derivatives than *Certhidea* or that there is more exchange between the various *Geospiza* species populations; both factors should have an influence on heterozygosity levels. (3) Indeed, interisland movements, particularly of *G. fortis* and *G. fuliginosa* but not *Certhidea,* are well known (Lack 1969, Harris 1973, Grant et al. 1975). Thus, effective gene flow, one expected consequence of which is increased $\bar{H}$ levels, is presumably greater in the *Geospiza* species than in *Certhidea.* Finally, (4) there is some suggestion that population sizes of *G. fortis* and *G. fuliginosa* are indeed larger than those of *Certhidea.* Dr. P. R. Grant (pers. comm.) has found a significant positive correlation between density estimates from netting programs and numbers of specimens in museum collections. It is thus possible to use the latter as a rough index of relative population sizes. In fact, where either, or both, *G. fortis* and *G. fuliginosa* co-occur with *Certhidea* (nine islands) they are on the average 3.5 times more common on any given island (data on museum collection numbers provided in Lack 1947: 168–185).

Although there is clear need for further study, the data available are certainly consistent with the hypothesis that within-population genic variation in the Galapagos finches is largely a function of population dynamics. A similar conclusion was

TABLE 5. Summary of interisland genetic similarity and distance values within species of Galapagos finches (SD = empirical standard deviation). $\bar{F}_{ST}$ is the mean variance in allele frequency across the sampled populations of each species.

| Species | Rogers' $\bar{S} \pm$ SD | Range | Nei's $\bar{D} \pm$ SD | Range | $\bar{F}_{ST}$ |
|---|---|---|---|---|---|
| *Geospiza fortis* | 0.956 ± 0.015 | 0.926–0.999 | 0.018 ± 0.012 | 0.048–0.002 | 0.0652 |
| *G. scandens* | 0.964 ± 0.004 | 0.960–0.968 | 0.005 ± 0.001 | 0.006–0.004 | 0.0197 |
| *G. fuliginosa* | 0.957 ± 0.013 | 0.923–0.981 | 0.015 ± 0.010 | 0.044–0.002 | 0.0544 |
| *G. difficilis* | 0.939 ± 0.005 | 0.935–0.944 | 0.021 ± 0.004 | 0.025–0.018 | 0.0570 |
| *G. magnirostris* | 0.964 ± 0.019 | 0.930–0.988 | 0.018 ± 0.019 | 0.050–0.001 | 0.0461 |
| *Camarhynchus parvulus* | 0.959 ± 0.019 | 0.921–0.981 | 0.019 ± 0.015 | 0.046–0.002 | 0.0574 |
| *Platyspiza crassirostris* | 0.964 ± 0.010 | 0.954–0.981 | 0.018 ± 0.009 | 0.029–0.004 | 0.0338 |
| *Certhidea olivacea* | 0.897 ± 0.049 | 0.824–0.956 | 0.090 ± 0.049 | 0.158–0.022 | 0.1248 |

reached in an examination of genic variation in introduced black rat (*Rattus rattus*) populations in the archipelago, where interisland movement patterns could be deduced from the historical pattern of human colonization (Patton et al. 1975).

*Within-species genetic similarity.*—Within the limitations of the data, the species of Galapagos finches appear little differentiated across the island populations sampled; the sole exception is the Warbler Finch (Table 5). For all but this one species, mean $S$-values are uniformly high (mostly above 0.950), and the range of variation is relatively small. *Certhidea,* however, exhibits somewhat marked interisland variation, being on the average nearly six times as differentiated as the other species examined. The level of within-species differentiation can also be measured by Wright's (1965) $F$-statistics, particularly $F_{ST}$, the standardized variance in allele frequencies across the populations sampled. Mean $F_{ST}$ values for the Galapagos finch species (Table 5) again emphasize the increased level of differentiation in *Certhidea* as compared to other species; the Warbler Finch is about three times more structured on geographic grounds than are other finch species.

Again, these data are reflected in the relative degree of morphological diversity within the species in question: each of the four island populations of *Certhidea* examined represents well-marked races, whereas racial differentiation has not been recognized for the other finch species (Lack 1969). Hence, most of both the within and between population variation appears explicable in terms of population size and degree of population isolation from conspecifics on other islands.

One might expect a concordance between interisland genic similarity and the distance between sampled islands or the degree of isolation of a given island, particularly if gene flow is an important contributor to the variation patterns observed. $S$-values showed no relationship, however, either to any of the various island isolation measures employed in previous studies (e.g. Hamilton and Rubinoff 1963, 1967) or to the straight-line distance between island pairs for either *G. fortis* or *G. fuliginosa,* the two most completely sampled species ($r < 0.529$ with $P > 0.25$ in all cases). On the other hand, there is also no relationship between $S$ for either species and a measure of habitat similarity between island pairs, such as the plant dissimilarity index of Preston (1962b) ($r < 0.149$, $P > 0.25$ in both cases), which might be suggestive of a selective force molding interisland similarity measures. Clearly, if gene flow is a dominant factor, interisland movements do not always proceed in a stepping-stone fashion across the archipelago. More likely, while the level of gene flow within the *Geospiza* species is probably sufficient to influence heterozygosity levels and overall interisland similarity patterns, it is not sufficiently

strong to override within-island drift from obscuring a similarity with distance relationship.

While within-population genic variation apparently shows no "island effect" (see above), the between-population measures of differentiation for the Galapagos finches are, in general, markedly higher than similar estimates for the few continental avian species as yet examined. Both Nei's $D$ and $F_{ST}$ are several times higher within the Galapagos species: within-species $\bar{D}$ across all finch taxa is 0.0255, and that for local populations to subspecies of mainland species is 0.0024–0.0048; $\bar{F}_{ST}$ is 0.0573 for Galapagos taxa, 0.0270 for mainland ones (comparative data from Barrowclough 1980).

*Between-species genic similarity.*—All in all, the geospizines form a tightly knit assemblage of taxa that share a high degree of overall genetic similarity (Table 6). The average similarity among species within the same genus is 0.957 ± 0.010 (empirical standard deviation) ($\bar{D}$ = 0.021 ± 0.016); in *Geospiza* the amount of interspecific differentiation is not different from the degree of intraspecific variation ($\bar{S}_{\text{within}}$ = 0.956, $\bar{S}_{\text{between}}$ = 0.944; $t_5$ = .002, df = 18, $P > 0.40$). Interestingly, while the levels of within-species island differentiation are three to four times larger than comparable measures for mainland species (see above), this does not translate into an increased interspecific divergence level. We interpret this to mean that divergence in structural genes is associated not with speciation, but with simple isolation of different island populations, in spite of some gene flow.

Species within geospizine genera display the same level of differentiation as do species of thrushes of the genus *Catharus* (Avise et al. 1980) but are only one-fifth as differentiated as are warblers of the genera *Vermivora, Dendroica,* or *Seiurus* (Barrowclough and Corbin 1978). Intergeneric differentiation is also rather low among the geospizines; $\bar{D}$ is only 0.079 ($\bar{S}$ = 0.890), as compared to an average $D$-value of 0.179 for wood warbler genera (Barrowclough and Corbin 1978) and 0.344 for thrush genera (Avise et al. 1980).

At the species level the sampling program was most thorough for the Small and Medium ground-finches (*G. fuliginosa* and *G. fortis,* respectively) in terms of both total numbers and percentage of island populations examined. Interestingly, at both James Bay on Isla Santiago and Academy Bay on Isla Santa Cruz, sympatric populations of these two species display more genic similarity to each other than either does to conspecific populations on other islands. At Academy Bay, *G. fortis* ($n$ = 11) and *G. fuliginosa* ($n$ = 8) share a similarity of 0.970, while the average similarity of Academy Bay *fortis* to other populations of the species is 0.956 ± 0.013 SD and of *fuliginosa* to other populations is 0.949 ± 0.013. Corresponding values for James Bay *fortis* ($n$ = 19) and *fuliginosa* ($n$ = 11) are 0.977, 0.952 ± 0.014, and 0.965 ± 0.009, respectively. These trends are not seen at other localities where both species were collected. While we cannot discount the fact that this observation may be an artifact of sample size, particularly because the level of interspecific divergence is not statistically different from that at the intraspecific level in *Geospiza* species, the possibility is raised of limited hybridization between the two species. This possibility has been suggested by several authors, including Lowe (1930, 1936) and Lack (1947, 1969), and needs to be investigated further.

*Phylogenetic relationships.*—A summary of the phenetic relationships among the geospizines is provided in Fig. 1a, a UPGMA phenogram based on Rogers' $S$-values. Partitioning the same data matrix by the maximum parsimony method of Farris (1972) or by that of Fitch and Margoliash (1967) yields virtually identical results

TABLE 6. Matrix of genetic similarities (Rogers' $S$-value) above the diagonal and genetic distances (Nei's $D$-value) below the diagonal for 11 species of Galapagos finches.

| | *Geospiza fortis* | *G. scandens* | *G. fuliginosa* | *G. difficilis* | *G. magnirostris* | *G. conirostris* | *Camarhynchus pauper* | *C. parvulus* | *Certhidea olivacea* | *Cactospiza pallida* | *Platyspiza crassirostris* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Geospiza fortis* | — | 0.947 | 0.974 | 0.965 | 0.964 | 0.925 | 0.905 | 0.916 | 0.835 | 0.868 | 0.890 |
| *G. scandens* | 0.014 | — | 0.941 | 0.921 | 0.925 | 0.896 | 0.889 | 0.900 | 0.819 | 0.852 | 0.878 |
| *G. fuliginosa* | 0.004 | 0.022 | — | 0.950 | 0.964 | 0.937 | 0.920 | 0.932 | 0.847 | 0.882 | 0.907 |
| *G. difficilis* | 0.005 | 0.028 | 0.009 | — | 0.950 | 0.937 | 0.894 | 0.904 | 0.832 | 0.863 | 0.882 |
| *G. magnirostris* | 0.015 | 0.049 | 0.007 | 0.017 | — | 0.944 | 0.922 | 0.921 | 0.853 | 0.888 | 0.906 |
| *G. conirostris* | 0.030 | 0.065 | 0.020 | 0.022 | 0.018 | — | 0.920 | 0.919 | 0.823 | 0.882 | 0.904 |
| *Camarhynchus pauper* | 0.060 | 0.076 | 0.041 | 0.064 | 0.051 | 0.050 | — | 0.974 | 0.861 | 0.950 | 0.935 |
| *C. parvulus* | 0.053 | 0.064 | 0.039 | 0.056 | 0.053 | 0.047 | 0.003 | — | 0.861 | 0.941 | 0.925 |
| *Certhidea olivacea* | 0.119 | 0.135 | 0.107 | 0.128 | 0.109 | 0.142 | 0.102 | 0.101 | — | 0.861 | 0.869 |
| *Cactospiza pallida* | 0.109 | 0.129 | 0.091 | 0.109 | 0.099 | 0.095 | 0.040 | 0.041 | 0.109 | — | 0.969 |
| *Platyspiza crassirostris* | 0.079 | 0.094 | 0.062 | 0.085 | 0.067 | 0.078 | 0.047 | 0.050 | 0.092 | 0.012 | — |

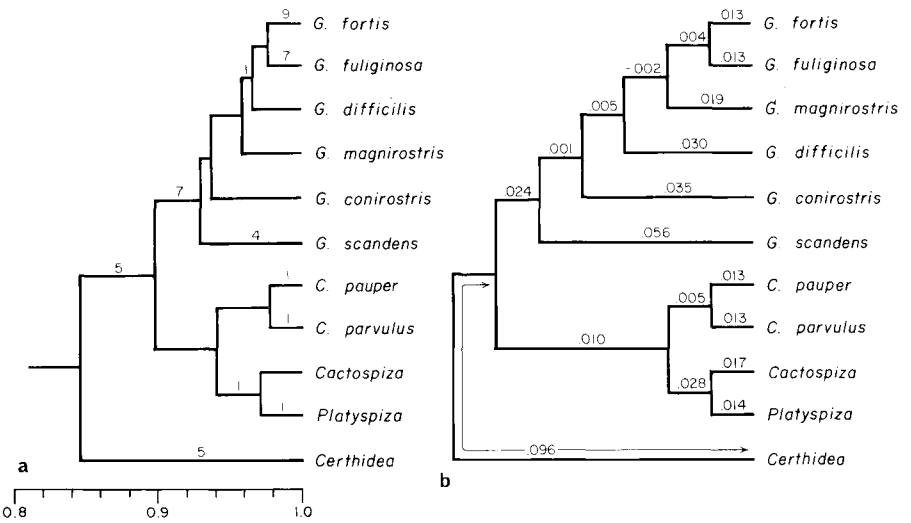


Fig. 1. Relationships among taxa of Galapagos finches based on (a) UPGMA phenogram of Rogers' similarity coefficients ($S$-values), where numbers along branches indicate the number of alleles unique to two or more of the terminal taxa connected by that branch; and (b) Fitch-Margoliash tree, with branch lengths given in Rogers' distance coefficients ($D$-value, which equals $1 - S$).

(Fig. 1b). Although none of these approaches yields rooted trees, a basic dichotomy does divide the Warbler Finch from the ground- and tree-finches, with subsequent division of the latter into a single lineage containing all members of *Geospiza* on the one hand and that containing the three genera/subgenera of tree-finches on the other. All analyses suggest a closer relationship between *Cactospiza* and *Platyspiza* as opposed to *Camarhynchus*. This is the only departure from the traditional view of geospizine relationships (Lack 1947, 1969). It is not a major disagreement, however; in fact, the relationships between the three genera of tree-finches should be considered unresolvable based on the overall level of shared similarity. Similarly, the true relationships among the six species of ground-finches cannot be resolved, because each differs only by frequency differences within the same set of alleles.

An examination of the distribution of alleles across the taxa supports the suggestions of relationship stated above. Of the 75 alleles detected across the 27 loci examined, 25 of these (33%) are shared by all 11 taxa; within the latter, 21 (84%) are the dominant allele in all species (Table 2). *Certhidea* owes its distinctness to five unique alleles (Fig 1a and Table 2), three of which are in relatively high frequencies (greater than 30%). The ground-finches as a genus contain seven unique alleles, but the tree-finches are quite poorly delimited. Interestingly, *G. fortis, G. fuliginosa,* and *G. scandens,* as species, are characterized by high numbers of unique alleles (9, 7, and 4 respectively, Fig. 1a). In each case the alleles in question are rare on a population basis (less than 5% in frequency). If this is not a sampling artifact, these data suggest that these species may maintain larger genetically effective population sizes than other finch species, and, at least for *G. fortis* and *G. fuliginosa,* the data are correlative to those on interpopulation divergence and heterozygosity levels, which suggest inter-island movements and hence larger populations.

The radiation of the Galapagos finches, as judged by the genic data, was quite

recent. Using the approximations as to substitution rate, molecule size, etc. suggested by Nei (1975), divergence times between species can be estimated as $t = 5 \times 10^6 D$ (where $D$ is Nei's $D$-value). While the assumptions relating to Nei's estimate are many and varied and while many factors involving the pattern of speciation may affect substitution rates in populations, calculated divergence times range from 570,000 yr (*Certhidea* versus other geospizines) to 62,500 yr for *Cactospiza-Platyspiza*. Even if corrections are made for the possibility that avian proteins evolve at a rate about one-third that of other vertebrates (Prager et al. 1974, Prager and Wilson 1975), these times are within the known geological age of the archipelago, for which dates ranging from about 4 million yr to less than one-half million yr have been determined (Cox and Dalrymple 1966, Cox 1971, Bailey 1976).

## CONCLUSIONS

Population size and the degree of interisland movements within species of finches appear to have a major influence on the patterns of genic variation exhibited by them. This conclusion is supported by the followng observations: (1) lack of interisland genic differentiation within the ground-finches, as exemplified by *G. fortis* and *G. fuliginosa*; (2) evenness in the distribution of mean population heterozygosity values in *Geospiza* species across islands of markedly different sizes and ecological characteristics; (3) the relationship of both (1) and (2) to the lack of taxonomic diversity within these species and to the known degree of interisland movements; (4) the high proportion of unique, rare alleles maintained in *Geospiza* species, suggesting large effective population sizes helping to maintain alleles introduced by mutation; (5) the positive relationship in *Certhidea* of mean heterozygosity to island size (and presumably population size?); and (6) the high degree of taxonomic diversification in *Certhidea* along with significantly higher interisland genic divergence levels and apparent lack of interisland movements.

Thus, genic variability patterns within and between the Galapagos finches are consistent with the view that allozyme differentiation more closely mirrors the history of population evolution and timing of species splits; it does not appear to be a component of the adaptive processes that produced the finch radiation in the archipelago. Certainly, there is no obvious direct relationship between genic patterns and environmental heterogeneity (floristic and food differences among islands) or interspecific competition patterns. This is opposed to the pattern in continuously varying morphological features such as beak shape and body size (Lack 1947, Bowman 1961, Grant et al. 1976, Abbott et al. 1977).

Finally, the genic data suggest both that the radiation of Galapagos finches was recent (an observation supported by the known age of the archipelago) and that the diversity of bill types and feeding behaviors was achieved without significant genetic change, at least as indexed by allozyme differentiation. The latter observation fits the growing body of inferential evidence that major morphological shifts during adaptive radiation are more likely to involve other than structural gene changes (e.g. Wilson 1976, Gould 1980).

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