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A New Perspective on The Evolutionary History of Darwin's Finches

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The 13 species of finches found on the Galápagos Islands, and the one species from Cocos Island, together collectively known as Darwin's finches, are one of the better-studied groups of birds. Much has been learned about their ecology, behavior, and the short-term effects of natural selection (Lack 1947, Bowman 1961, Grant 1999). The four species of tree finch (*Camarhynchus*), six species of ground finch (*Geospiza*), the tool-using Woodpecker Finch (*Cactospiza pallida*), the Vegetarian Finch (*Platyspiza crassirostris*), the Warbler Finch (*Certhidea olivacea*), and the finch on Cocos Island (*Pinaroloxias inornata*) appear to fill different ecological roles via differentiation of bill size and shape (Grant and Grant 2002). In fact, most authors consider Darwin's finches to be a classic example of an adaptive radiation, owing to the great diversity in bill form and ecological habit that presumably evolved in a relatively short time. For example, Petren et al. (1999:321) noted, "Species in this group show adaptive variation in beak size, beak shape and body size that is more typical of differences among [taxonomic] **families** of birds. . . ." (boldface added).

Taxonomic History.—Darwin originally collected the finches from the Galápagos, not realizing what an evolutionary gold mine they would become (Sul-loway 1982). In fact, he was not careful about labeling specimens as to the island from which a specimen was obtained, thus obscuring taxonomic boundaries. Subsequent work with better-labeled specimens revealed taxonomically significant patterns of variation. Gould (1837) recognized that different species existed in the collections from the Darwin expedition. However, Gould was unable to produce a stable classification. Since Gould's time, many of the major figures in avian taxonomy have published differing classifications. The succession of revisionary efforts attests to the difficult nature of classifying phenotypic variation among the finches. Although the species show considerable morphological diversity, many in fact are notoriously difficult to identify in the field (especially females and immatures). Populations from different species and islands overlap in morphometric space (Grant 1981).

Not surprisingly, there has been considerable controversy over specific and especially generic limits. For example, a series of specimens from James Island was consecutively classified as *Cactornis hypoleuca* (Ridgway 1890), *Camarhynchus pallidus* (Ridgway 1896), *Geospiza pallidus* (Rothschild and Hartert 1899, Sharpe 1909), *Cactospiza pallida pallida* (Swarth 1931, Hellmayr 1938, Lack 1945), and *Camarhynchus pallidus pallidus* (Lack 1969, Paynter 1970). Of the total of 67 taxonomic names proposed at the species or subspecies level, 32 survived in Paynter's (1970) widely used list, with recent authors recognizing 14 species.

Attempts at a Finch Phylogeny.—Such taxonomic flux portends a complex evolutionary history and a concomitant difficulty in arriving at a definitive phylogenetic hypothesis. Lack (1947) constructed a now famous "tree" (see fig. 2 in Grant and Grant 2002) that was based on his understanding of the bird's morphology and ecology. An allozyme analysis by Yang and Patton (1981) produced two somewhat conflicting genetic distance trees; reanalysis by Stern and Grant (1996) yielded no substantive changes. Application of quantitative genetic techniques yielded another tree (Schluter 1984). Those studies, based on traditional morphological features or distance analyses, did not yield trees that would be considered robust phylogenetic hypotheses by today's standards.

DNA to the Rescue?—One might expect that phylogenetic analyses of DNA sequences would resolve our understanding of the evolutionary history of Darwin's finches. A resolved phylogeny would cast the wealth of ecological and behavioral information in its proper phylogenetic context (Harvey and Pagel 1991). Three DNA studies based on the same blood samples now exist (unfortunately voucher specimens were unavailable). Two research groups independently analyzed mitochondrial DNA (mtDNA) sequences (Sato et al. 1999, Freeland and Boag 1999a, b), and one of those groups (Freeland and Boag 1999b) also explored a nuclear gene. The two mtDNA studies were largely redundant and I refer mostly to the Sato et al. (1999) study, which included all species simultaneously. The nuclear gene lacked phylogenetic resolving power owing to low variability that is typical of nuclear genes at that taxonomic level

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(Palumbi et al. 2001). A third group analyzed microsatellite allele frequencies (Petren et al. 1999). MtDNA and microsatellites exhibited sufficient variability to allow assessment of how the variation was apportioned phylogenetically. The two types of data yielded different phylogenetic hypotheses, although nodal support in each tree is weak, thereby tempering the actual degree of incongruence.

Several conclusions about finch phylogeny emerge from the mtDNA and microsatellite studies. Both data sets support the existence of six clades: *Geospiza*, *Camarhynchus*, *Platyspiza*, *Cactospiza*, *Pinaroloxias*, and *Certhidea*. Although several interesting phylogenetic conclusions emerge from the data sets, the biggest surprise of the mtDNA studies was the lack of differentiation and reciprocal monophyly among species in *Geospiza* and *Camarhynchus*.

Comparisons of Species Within *Geospiza* and *Camarhynchus*.—MtDNA sequences (Sato et al. 1999) from different species within those genera are extremely similar, ranging from 0 to 1.2% in *Geospiza* and 0.2 to 1.3% in *Camarhynchus*. A genetic distance of “0” between individuals of supposedly different, highly morphologically divergent species of Darwin’s finch is unexpected; even phenotypically similar avian sister species differ by 1% or more (Avise and Walker 1998). The intra- and interspecies mtDNA distances greatly overlap, and the intergeneric distances rival those of comparisons within other avian genera. Most surprisingly, there is extensive paraphyly at the species level in both *Geospiza* and *Camarhynchus* (Fig. 1). That is, from a mtDNA sequence of an individual identified phenotypically as a *Geospiza*, one could not identify which of the six putative species from which it was obtained. For example, a tree (not shown) derived from control region sequences deposited in Genbank by Sato et al. (1999) reveals that a haplotype from a *G. magnirostris* sampled on Santa Cruz is more closely related to haplotypes from *G. scandens* (Marchena) and *G. difficilis* (Genovesa) than to another *G. magnirostris* from Santa Cruz. A haplotype from a *G. conirostris*, a species with a mass of 28 g (Petren et al. 1999) is closer to one from a *G. fuliginosa* (14 g) than to other *G. conirostris*. The same is true for individuals identified phenotypically as members of *Camarhynchus* (*sensu* Paynter 1970).

To emphasize the peculiar nature of these mtDNA data, one might realize that the set of sequences that represent individuals of all six *Geospiza* species is very similar to a set of sequences one might draw from a single randomly mating population of another bird. Using the 29 control region sequences for the six species of *Geospiza* from the Genbank entries deposited by Sato et al. (1999), F_{st} for the six species-level taxa was 0.002, not significantly different ($P = 0.41$) from zero. Grouping specimens by island, irrespective of species designations, F_{st} was 0.005, also insignificant ($P = 0.38$). A common way to analyze mtDNA sequences taken from a population is to

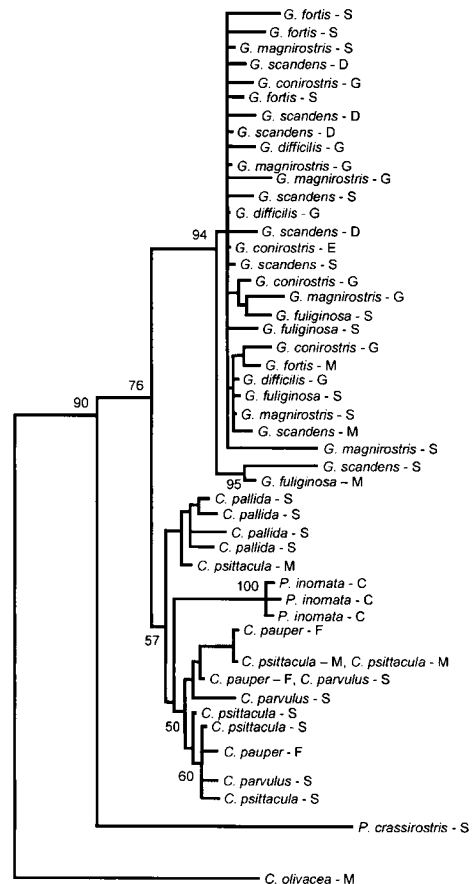


FIG. 1. Neighbor-joining tree derived from mtDNA sequences, redrawn from Sato et al. (1999), excluding multiple samples of *C. olivacea* and *P. crassirostris*; branch lengths are proportional to Tamura-Nei genetic distance. Letters represent islands from which individuals were sampled: C = Cocos Islana, S = Santa Cruz, D = Daphne Major, E = Espanola, F = Floreana, G = Genovesa, M = Marchena. Numbers represent percent bootstrap support (out of 500 replicates). Topology rooted with two sequences from *Tiaris obscura*.

compute a mismatch distribution, which is simply all pairwise differences among individual's sequences plotted as a function of number of base-pair differences. This distribution is typically unimodal if the population has been growing, or “ragged” if it has been stationary (Harpending et al. 1998). An example of a mismatch distribution for a growing conspecific population is that for the Curve-billed Thrasher (*Toxostoma curvirostre*; Fig. 2). The mismatch distribution for the 29 *Geospiza* control region sequences (Fig. 2) is unimodal and similar in shape to that for the thrashers. Typically, such a plot for different spe-

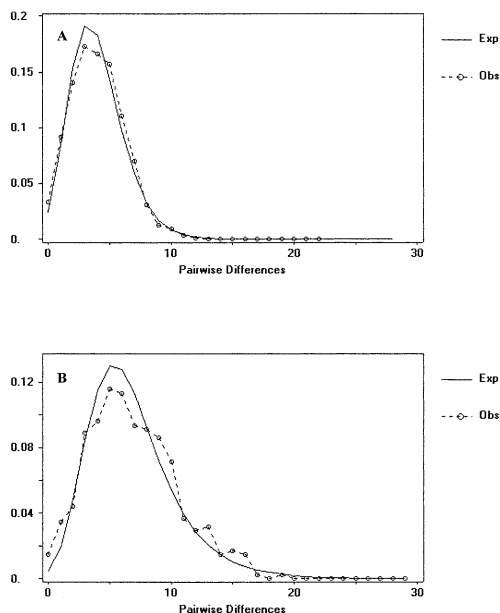


FIG. 2. Mismatch distributions for mtDNA sequences representing individual Curve-billed Thrashers (A) (Zink and Blackwell 2000) and specimens of all species of *Geospiza* (B).

cies should be clearly bi- or multimodal, with the peaks corresponding to comparisons within and between species. Similarly, the degree of nucleotide diversity for those 29 *Geospiza* sequences representing six putative species, 0.007, is equivalent to that computed for single populations. The nucleotide diversity, mismatch distribution, and F_{st} value are consistent with the hypothesis that those sequences were drawn from a relatively young conspecific population that has undergone recent growth, and not what one would expect for mtDNA sequences representing six species on independent evolutionary trajectories.

The F_{st} value for *Camarhynchus* (*C. psittacula*, *C. parvulus*, *C. pauper*) was -0.03 ($P = 0.59$). Although the mismatch distribution (not shown) had two peaks, it was not significantly different ($P = 0.2$) from that expected for an expanding population. Given the small number of species (3) and sequences, the conclusions reached below concerning *Geospiza* also tentatively apply to *Camarhynchus*.

The microsatellite results potentially complicate the issue. Petren et al. (1999) show a fully resolved tree (Fig. 3), a result that conflicts with the mtDNA tree. Microsatellite alleles, being nuclear in origin, should take longer to coalesce than mtDNA haplotypes because of the greater effective population size of nuclear genes (Moore 1995). Theory shows that most nuclear loci will show monophyly only when the branch length leading to the mtDNA sequences

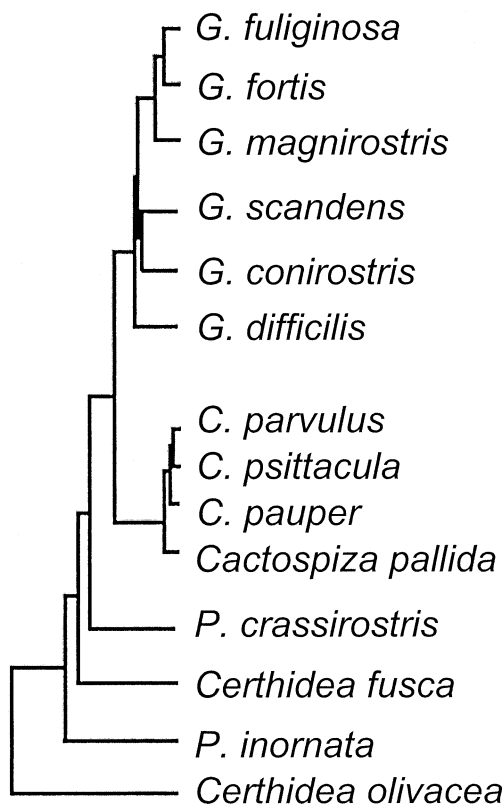


FIG. 3. Branching diagram (UPGMA method) derived from microsatellite DNA length variation (redrawn from Petren et al. 1999). Branch lengths proportional to genetic distance.

of a taxon is $3\times$ longer than the average mtDNA sequence diversity within the taxon (Palumbi et al. 2001), which is clearly not the case in *Geospiza* or *Camarhynchus*. If the mtDNA tree is unresolved (and shows massive paraphyly), so should the microsatellite tree. Furthermore, the danger in inferring genealogy from microsatellite data is well known (Page and Holmes 1998).

An answer to the discrepancy between data sets likely lies in Petren et al.'s (1999) method. They pooled large numbers of individuals, calculated allele frequencies, and computed distances between *a priori* defined groups. Hence, by assuming species limits, the problem of alleles not sorting according to taxonomic species boundaries was inadvertently masked. The large number (16) of loci also contributed to resolving some nodes. Nevertheless, many of the nodes are extremely closely placed in the microsatellite tree, and it seems likely that many individual specimens could not be unambiguously sorted to species by the microsatellite alleles they possess. A recent extensive microsatellite analysis (Grant et al. 2000) failed to support the monophyly of *G. difficilis*,

although it was depicted as being monophyletic in the tree (Fig. 3) published by Petren et al. (1999). Therefore mtDNA and microsatellite results likely agree that there are no unambiguous genetic clusters within *Geospiza* or *Camarhynchus* that correspond to recognized species limits.

Hypotheses to Explain DNA Similarity Among Species and Paraphyly.—Lack of reciprocal monophyly among all six species of *Geospiza* (Fig. 1) is uncharacteristic of nearly all other avian species and genera (see Ellsworth et al. 1994). One expects occasionally to discover a lack of reciprocal monophyly between recently isolated sister taxa, but not among all six species in a morphologically well-differentiated genus (see Klicka et al. 1999). Observed paraphyly could have several causes.

Recency of Speciation.—An often-used acid test of evolutionary independence is the existence of reciprocal monophyly in mtDNA haplotype trees. Reciprocal monophyly means, phylogenetically, that haplotypes in a taxon are more closely related to each other than any is to haplotypes in another clade. Therefore, one could identify an individual's evolutionary lineage from its sequence. However, there is a "lag time" before reciprocal monophyly is evident in phylogenetic trees of mtDNA haplotypes sampled from recently isolated species. Lag time is defined by coalescence theory (Hudson 1990) as $2N_e$ generations on average, where N_e is the inbreeding effective size of the female population.

Estimating the lag time to reciprocal monophyly for species of *Geospiza* is complicated by gene flow, hybridization, and identification of the appropriate breeding group of individuals: an island population, a "species" or the entire genus. A generation length is 1–2 years for most passerines, although Grant and Grant (1992) suggested a much longer time (5–6 years) for *G. fortis* and *G. scandens*; however, their calculations from a single small island of two cohorts of birds revealed a high variance (and in several instances, finches <1 year old have bred). N_e values from the literature for other birds range from <1,000 (Baker and Marshall 1999) to 50,000 (Ball and Avise 1992). N_e can be estimated as $\theta = 2N_e\mu$. The estimated θ for control region sequences (Sato et al. 1999) of all *Geospiza* sequences is 0.0063, and assuming a mutation rate (μ) of from 1 to 4×10^{-7} for mtDNA control region sequences (Baker and Marshall 1999), N_e ranges from 7,875 to 31,500 (if the "population" has been rapidly growing the coalescence time could be older). Given these figures, the ancestral haplotype ("Eve") of *Geospiza*, that is the coalescence point for the haplotypes for the entire genus, would date to 15,750 to 63,000 years before present (longer if generation times are longer). However, the coalescence point of haplotypes precedes the actual point of lineage separation (speciation) by a considerable factor, although the exact amount is debatable (Avise and Walker 1998, Klicka and Zink

1999). Assuming that the species are actually isolated, the actual time of lineage isolation would be even more recent. These analyses suggest an extremely recent common ancestor for sequences in the genus.

Nuclear Copies.—One possibility is that the mtDNA sequence data are actually from nuclear copies (numts) of mitochondrial genes (Zhang and Hewitt 1996); nuclear copies evolve more slowly than mt copies. The samples used for mtDNA studies lend credence to that possibility. Most DNA was extracted from blood, which in birds contains high levels of nuclear DNA, and numts are often found (Sorenson and Quinn 1998). In fact, Sato et al. (1999) discovered numts, some of which appear quite old (Sato et al. 2001). However, most individuals have distinct but very closely related haplotypes, which is an unexpected consequence of nuclear copies. Second, one expects some true mitochondrial copies to be discovered, which would appear as a few divergent branches. Many sets of primers were used, long sequences were amplified, and coding sequences did not exhibit stop codons. These factors argue against numts.

Hybridization.—Another explanation for the lack of reciprocal monophyly in mtDNA, and similar microsatellite allele frequencies, is hybridization. The finches are known to hybridize (Grant 1999, Grant and Grant 1994) and Lowe (1936) suggested that the finches represented a "swarm of hybridization segregates." Both Sato et al. (1999) and Freeland and Boag (1999a, b) concluded that hybridization plays a major role in the evolution of the finches, and partially explains why haplotypes do not sort according to recognized species limits. Inspection of the tree (Fig. 1) derived from mtDNA sequences reveals that there would have to be hybridization between most if not all pairs of phenotypes, which might not be unrealistic. On the small island of Isla Daphne Major, Grant and Grant (1992:781) noted, "In an average breeding year a little less than 1% of breeding *G. fortis* pair with resident *G. scandens* and produce viable and fertile offspring. . .", and "Hybridization with immigrant *G. fuliginosa* (Small Ground Finch) occurs at three times this rate and with the same high success." Consistent with that observation, Freeland and Boag (1999b) found a haplotype that occurred in *G. fuliginosa*, *G. magnirostris*, *G. scandens*, and *G. difficilis*. Thus, the evolutionary integrity of taxa is in doubt, because those figures reveal gene flow across species boundaries that exceeds that expected for populations to be isolated (Wright 1978). Hybridization could explain the sharing of haplotypes across morphologically defined "species" boundaries (but not the shallowness of the tree; see below).

Selective Sweeps.—The rapid fixation of a new selectively superior haplotype can "reset" the mitochondrial clock in a species (Page and Holmes 1998). Such a hypothesis seems unlikely to explain the observed haplotype tree, because of the high number of haplotypes. Nonetheless, it is difficult to eliminate

this hypothesis entirely, because the extremely shallow depth of the haplotype tree is a striking feature of these data. Also, if hybridization is very frequent, a selectively superior haplotype could spread and become fixed among species. If the lack of genetic differences among species were due to a selective sweep, the amount of hybridization among *Geospiza* species would probably be of a magnitude sufficient also to preclude the existence of genetic species boundaries.

Synthesis.—All recent data sets support the existence of six clades of Darwin's finches, including *Pinaroloxias*, *Cactospiza*, *Platyspiza*, *Camarhynchus*, *Geospiza*, and *Certhidea* (which might be two, nonsister clades). The node uniting those taxa is relatively recent (<3% sequence divergence) and is in fact consistent with most nodes uniting species of a single avian genus. In contrast, an avian adaptive radiation consisting of nine species of Malagasy birds has an average sequence divergence of $11.2 \pm 3.1\%$ (Cibois et al. 2001) in mtDNA cytochrome-*b*, a more slowly evolving gene than the control region. The entire group of Darwin's finches indeed appears to be of recent origin, as predicted by most authors, which is consistent with a relatively young age for the islands. Thus, at the level of these six clades, we see the characteristic imprints of one view of an adaptive radiation: much morphological and ecological divergence superimposed over a shallow mtDNA history indicating recent taxon origination.

Past authors have considered individual species of *Geospiza* and *Camarhynchus* as participants in the radiation, and have concentrated on the great degree of bill-size evolution, especially in *Geospiza*. Given the mtDNA tree, F_{st} -values, degree of hybridization, and the fact that phenotypes of taxa overlap in multivariate space (Grant 1981), there is little evidence for clear species limits within *Geospiza* or *Camarhynchus* (sensu Paynter 1970), irrespective of whether one uses biological, phylogenetic, genealogical, or evolutionary species concepts. Granted, it makes sense that if the six major groups are closely related, the species within those groups should be even more closely related. However, the currently recognized species of *Geospiza* would not even qualify as evolutionarily significant units (Moritz 1994), one of the least inclusive taxonomic units considered for protection by conservation biologists. Thus the question is whether species in those genera are in fact isolated and "behaving" as species but not yet reciprocally monophyletic because of the inherent lag time, or whether the unstable taxonomic history of the finches is now understandable.

Sato et al. (1999), Freeland and Boag (1999a, b) and Grant and Grant (2002) do not question the existence of species of *Geospiza* or *Camarhynchus*. In fact, Sato et al. (1999) selected a single haplotype from each species for their final phylogenetic estimate, thereby producing a tree (their fig. 5) that masks the lack of

monophyly for all species of *Geospiza* and *Camarhynchus*. They favor the interpretation that all the species are too recently evolved to exhibit reciprocal monophyly, and that hybridization further mixes haplotypes among species. That view requires that strong selection on phenotypes counteracts the effects of hybridization and gene flow (finches of the same "species" move among islands), and is maintaining the very young morphologically defined species on independent evolutionary trajectories. Most importantly, this classical model of speciation predicts that given sufficient time into the future each species would become reciprocally monophyletic (depending on the degree of hybridization).

Evidence in support of this classical model is that songs appear to be fairly consistent among populations identified to species (Ratcliffe and Grant 1985). The possibility of cultural transmission means that songs might be stable over short periods, promoted by assortative mating (Grant and Grant 2002), yet unstable over the evolutionary times required to enforce the genetic integrity of taxa. The same lack of genetic differentiation accompanies avian song dialects (Zink and Barrowclough 1984). There appears to be assortative mating between some phenotypes, leading some to conclude that the taxa might be biological species (Grant 1999). The high degree of hybridization suggests that reproductive isolation is not a hallmark of these taxa, thereby requiring a very relaxed definition of biological species.

Evidence exists contrary to predictions of the classical model. Although lack of reciprocal monophyly is an expected consequence of very recent divergence, if those taxa have been isolated for any length of time, haplotypes should not be shared across species, which they are. One also expects a significant F_{st} value, which was not observed, irrespective of whether the sequences were grouped by species or island. Thus, the six species of *Geospiza* and three species of *Camarhynchus* do not resemble species from other avian genera.

There is an alternative to the viewpoint that species of *Geospiza* and *Camarhynchus* originated too recently to show reciprocal monophyly in haplotype trees—each genus is a polymorphic species. A novel model envisions multiple *Geospiza* niches throughout the islands, dictated largely by the food resource. Strong natural selection (Boag and Grant 1981) would maintain phenotypic differences among "taxa" in spite of inter-island dispersal of individuals from differing phenotypes. In the event of local extirpations, colonists from different phenotypic backgrounds fill those niches, and the observed distributions (Grant 1981) of finch morphologies are "reinvented" (Schluter and Nagel 1995) or fine-tuned to seed size. The speed at which finch bill morphologies can be sorted by natural selection is well documented (Grant 1999, Smith 1993). As long as the niches themselves are relatively stable across islands,

the resulting morphological patterns would mimic the existence of multiple species. In this view, the currently recognized taxa are morphotypes (with relatively fuzzy boundaries; Grant 1981) that are ephemeral in evolutionary time. A large-billed type on one island is not part of the same evolutionary lineage as a large-billed type on another island, because each was derived from individuals of different genetic and phenotypic backgrounds. The morphological groups on islands are in effect transient in evolutionary time. Morphological similarity is therefore not an accurate predictor of shared evolutionary history. Thus, *Geospiza* and *Camarhynchus* could each be functioning as single, highly variable species over evolutionary time. That view is consistent with the mtDNA hybridization and morphometric data.

These two hypotheses cannot be discriminated with the evidence at hand. The lack of reciprocal monophyly across multiple species, the sharing of haplotypes across species, and the high degree of hybridization and conspecific gene flow make it unlikely that the current recognized species of *Geospiza* and *Camarhynchus* are functioning as species in the traditional sense of taxa that are isolated, genetically or reproductively. That makes previous taxonomic instability understandable: if morphological differences among taxa have an ecological instead of an evolutionary bias, one does not expect stable taxonomic boundaries.

Such an evolutionary history has consequences for the many studies of these birds. Conclusions from many ecological and behavioral studies are likely not affected by this new interpretation. Findings based on a single morphologically defined population from a single island would likely be robust. However, evolutionary inferences could well be compromised. Grant and Grant (2002) plot a species accumulation curve versus the timing of island formation; that assumes an evolutionary basis to recognized species of *Geospiza* and *Camarhynchus*. Petren et al. (1999) state "species that root basally on the tree. . . have long, pointed beaks." They further extend that observation to the genera *Geospiza* and *Camarhynchus*, suggesting that bill evolution first follows lines of allometry, followed by differentiation in size. Considering the mtDNA and microsatellite data jointly, there is no phylogenetic resolution that would permit this inference. Sanderson (2000) found that the phylogeny based on microsatellites (Petren et al. 1999) did not explain the pairings of finches with different beak sizes on islands—that might be because the units of evolution are not equivalent to currently recognized species; there are many fewer degrees of freedom. Grant et al. (2000) explored aspects related to the allopatric phase of speciation of *G. difficilis*, although because the data did not recover the monophyly of populations of that presumed species, the evolutionary interpretation of this study is unclear (i.e. the allopatric origin of a paraphyletic species). Other evo-

lutionary inferences (Podos 2001) based on the standard view of *Geospiza* and *Camarhynchus* species could be affected.

The next step is to expand the mtDNA data set and verify its mitochondrial authenticity. Large samples of *Geospiza* and *Camarhynchus* from multiple islands should be surveyed for larger sequences and analyzed using coalescence theory. Additional independent loci would provide tests of the mtDNA data. Given the lack of mtDNA differentiation, it will be difficult to find nuclear sequences that will provide phylogenetic resolution (Palumbi et al. 2001). Additional morphological work, with attention to voucher specimens and measurement error, is also needed. Lastly, experiments involving crosses of small and large billed finches in a setting with an intermediate-sized seed resource would be informative. Until then, the current species-level taxonomy of *Geospiza* and *Camarhynchus* should be considered unresolved, and the null hypothesis ought to be that each is a single highly variable species over evolutionary time. Thus, only half as many species of Darwin's finches exist as previously thought.

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