Hybridization in the Recent Past

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ABSTRACT: The question we address in this article is how hybridization in the recent past can be detected in recently evolved species. Such species may not have evolved genetic incompatibilities and may hybridize with little or no fitness loss. Hybridization can be recognized by relatively small genetic differences between sympatric populations because sympatric populations have the opportunity to interbreed whereas allopatric populations do not. Using microsatellite DNA data from Darwin's finches in the Galápagos archipelago, we compare sympatric and allopatric genetic distances in pairs of *Geospiza* and *Camarhynchus* species. In agreement with the hybridization hypothesis, we found a statistically strong tendency for a species to be more similar genetically to a sympatric relative than to allopatric populations of that relative. Hybridization has been studied directly on two islands, but it is evidently more widespread in the archipelago. We argue that introgressive hybridization may have been a persistent feature of the adaptive radiation through most of its history, facilitating evolutionary diversification and occasionally affecting both the speed and direction of evolution.

Keywords: Darwin's finches, microsatellites, introgression, sympatry versus allopatry, sympatric speciation, adaptive radiation.

A resurgence of interest in the role of introgressive hybridization in evolution has occurred in the last 15–20 years (Arnold 1997, 2004; Dowling and Secor 1997; Ellstrand 2003). It is now known to be much more widespread taxonomically and geographically than formerly believed, and the genetic and fitness consequences have been determined in several plant and animal systems (Abbott 1992; Arnold 1992; Grant and Grant 1992; Dowling and

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DeMarais 1993; Rieseberg and Wendel 1993). A major contribution from breeding programs has been the demonstration of how novel and advantageous combinations of genes can be produced by transgressive segregation in hybridizing species (Rieseberg et al. 2003a, 2003b). A repeated finding from field studies is substantial introgression of some genes but not others (Cathy et al. 1998; Kim and Rieseberg 1999; Whitham et al. 1999; Sattler and Braun 2000; Martinsen et al. 2001; Sota 2002; Sullivan et al. 2002; Rieseberg et al. 2003b). Often the exchange of genes between species is unequal (Bacilieri et al. 1996; McDonald et al. 2001; Thulin and Tegelström 2002), with a tendency for genes to flow predominantly from common to rare species (Dowling et al. 1989; Taylor and Hebert 1993; Wayne 1993). Hybridization is therefore of interest to evolutionary biologists because partial and unequal gene exchange can have important effects on the dynamics of hybrid zones, speciation, and adaptive radiation (Chiba 1993; Grant 1998; Schluter 2000; Sætre et al. 2001; Bensch et al. 2002; Ortíz-Barrientos et al. 2002; Rieseberg et al. 2003b; Servedio and Sætre 2003; Gee 2004; Seehausen 2004).

Where phylogenies can be established with a system of neutral genetic markers, it is possible to determine the effects of introgression by reconstructing the transfer of genetic and phenotypic characters from one lineage to another (Dowling et al. 1989; DeMarais et al. 1992; McDade 1992; Andersson 1999; Matos and Schaal 2000; Sota et al. 2001; Allender et al. 2003; Feder et al. 2003). For groups of organisms that have recently diversified rapidly and are perhaps continuing to do so, establishing phylogenetic connections (in the absence of hybridization) is not easy because genetic differences are small and lineage sorting has not progressed far (but see Allender et al. 2003). Compounding the difficulties, introgressive hybridization occurring after speciation has begun can blur the small nascent genetic differences (Patton and Smith 1994; Clarke et al. 1998).

The question we address in this article is how hybridization in the recent past can be recognized with selectively neutral genetic data. The question is challenging. Two sympatric populations of a related group of organisms are genetically similar to a degree that may be a function of

both common ancestry and genetic exchange after their initial divergence. The question then is how the consequences of genetic exchange can be distinguished from the effects of common ancestry. A solution we explore here lies in the comparison of sympatric and allopatric populations of the same species. Sympatric populations have the opportunity to interbreed; allopatric populations do not. In the absence of interbreeding, sympatric populations of two species should be no more similar to each other genetically than each one is to allopatric populations of the other. In contrast, the introgression hypothesis predicts that a species is more similar genetically to a sympatric relative than to allopatric populations of that relative, as a result of exchanging alleles.

Recent adaptive radiations are useful systems for adopting this approach to the question of detecting evidence of past introgressive hybridization. They typically comprise several independent populations of the same species, which is a useful feature for making multiple comparisons for statistical purposes (Schluter and Nagel 1995; Losos et al. 1998; Chiba 1999; Rüber et al. 1999; Allender et al. 2003; Gillespie 2004; McKinnon et al. 2004), and the species are often not completely reproductively isolated from each other (Grant and Grant 1997*a*; Price and Bouvier 2002; Mendelson 2003). Especially useful are the radiations in archipelagos where a prima facie case can be made for allopatric speciation on geographical grounds alone (Wagner and Funk 1996; Grant 1998; Schluter 2000). In this article, we use genetic data from Darwin's finch species on the Galápagos islands. We apply the method of comparing sympatric and allopatric populations to several pairs of species, find evidence of introgressive hybridization, and in the "Discussion" consider the evolutionary implications of hybridization and its relevance to sympatric speciation.

Study System

Mitochondrial DNA and allozyme data suggest that Darwin's finches shared a common ancestor 2–3 million years ago (Grant 1999; Sato et al. 1999; Grant and Grant 2002*a*). Since then, a minimum of 14 species were formed. They have been classified on morphological grounds (Lack 1945, 1947) as ground finches (*Geospiza*; six species), tree finches (*Camarhynchus* sensu lato = *Camarhynchus* + *Cactospiza*; five species), warbler finch (*Certhidea*; one or two species; Petren et al. 1999; Grant and Grant 2002*b*), vegetarian finch (*Platyspiza*; one species), and Cocos finch (*Pinaroloxias*; one species). Studies of allozymes (Yang and Patton 1981), microsatellites (Petren et al. 1999), song (Bowman 1983), and breeding (Grant 1999) have largely supported the morphological classification, whereas mitochondrial DNA (*cyt b*) and nuclear internal transcribed

spacer genes have provided ambivalent support (Freeland and Boag 1999; Sato et al. 1999). Populations occur on one to more than 20 islands in various combinations (Grant 1999). Interbreeding of some species has been suspected on grounds of morphological intermediacy (Lack 1945, 1947; Bowman 1961, 1983). Several populations of ground finches are unusually variable in beak dimensions (Lack 1945, 1947; Bowman 1961; Grant and Grant 2000), and some of these populations are known to hybridize (Grant 1999). Interbreeding of ground finch species has been studied on two islands for many years (Grant and Grant 1989, 2002*c*; Grant et al. 2004). The F_1 hybrid and backcross individuals have been found to experience high fitness under favorable environmental conditions, with no indication of sterility or inviability (Grant and Grant 1992, 1998). We concentrate on the ground finch species (except for the oldest species, *Geospiza difficilis*, because relationships among populations of this species are uncertain; Grant et al. 2000) and also on the unique population of *Geospiza conirostris* on Española (Petren et al., forthcoming). There are too few populations (<6) of individual tree finch species for statistical analyses by binomial tests, the principal test we use; therefore, we have combined the species in a single analysis.

Methods

Details of collecting and genotyping procedures have been published elsewhere (Petren 1998; Petren et al. 1999; Grant et al. 2001). A total of 42 populations were studied, and sample sizes per population varied from four to 59 individuals (table 1), with a mean of 17.4. For comparing genetic differences between sympatric and allopatric populations of related species, we use Nei's genetic distance (*D*; Nei 1972) calculated from allele frequencies at 16 microsatellite loci. We use Nei's *D* rather than diversity-based distances such as *Fst* because, by taking allele identity into account, it is more appropriate when there has been recent admixture between species (Hedrick 1999). The genetic distance between species *i* and species *j* on island *k*, the *ik-jk* distance, is compared with allopatric distances *ik-jm . . . p* for species *i* and *jk-im . . . p* for species *j*. The subscript *m . . . p* refers to all other islands occupied by species *i* or *j*. The null hypothesis is that there is no difference between the sympatric distance *ik-jk* and the allopatric distances with which it is compared. Because we are concerned with the direction of differences between sympatric and allopatric distances and not with their magnitude, we use two-tailed binomial tests applied to pairs of species identified by morphology (Lack 1947; Schluter 1984), allozymes (Yang and Patton 1981), and microsatellites (Petren et al. 1999) as close relatives.

There are two ways to make the comparisons: a sym-

Table 1: Number of genotyped individuals (*N*), mean number of alleles (*A*), and mean observed heterozygosities (*H*$_o$)

Species and island	*N*	*A*	*H*$_o$
Geospiza fuliginosa:			
Daphne	28	9.6	.66
Santa Cruz	24	10.5	.72
Santiago	19	9.4	.74
Rábida	10	6.4	.68
Española	10	6.8	.68
Floreana	10	6.6	.72
San Cristóbal	21	8.7	.77
Pinta	10	5.8	.76
Isabela	13	7.6	.69
Geospiza fortis:			
Daphne	59	8.2	.63
Santa Cruz	39	10.4	.67
Santiago	9	6.2	.66
Marchena	17	6.1	.60
San Cristóbal	4	4.4	.76
Pinta	12	6.7	.74
Isabela	11	7.1	.71
Geospiza magnirostris:			
Daphne	54	6.2	.60
Santa Cruz	12	6.8	.61
Genovesa	32	6.6	.54
Rábida	5	4.2	.57
Marchena	10	5.1	.62
Pinta	7	4.1	.63
Fernandina	9	5.9	.60
Isabela	6	4.9	.60
Geospiza scandens:			
Daphne	52	6.1	.66
Santa Cruz	23	9.0	.61
Santiago	4	4.5	.77
Rábida	12	5.0	.61
Marchena	6	4.1	.55
San Cristóbal	6	4.9	.74
Genovesa	48	6.5	.59
Camarhynchus pallida:			
Santa Cruz	27	4.4	.38
Isabela	13	3.4	.41
Camarhynchus parvulus:			
Santa Cruz	18	5.9	.49
Floreana	22	6.1	.51
Isabela	7	4.4	.51
Camarhynchus psittacula:			
Santa Cruz	5	3.1	.48
Pinta	8	2.8	.45
Fernandina	5	3.6	.51
Isabela	4	2.7	.45
Camarhynchus pauper:			
Floreana	19	5.1	.49
Camarhynchus heliobates:			
Isabela	12	2.6	.31

Note: The *G. conirostris* population on Genovesa has been included with *G. scandens* because of their genetic similarity (Petren et al., forthcoming). *H*$_o$ at 16 microsatellite loci.

patric distance between two species may be compared with allopatric distances for each species separately or together. Each has the disadvantage of using some of the data twice, and therefore we present both sets of results. For the analysis of species considered one at a time, the genetic distance between a pair of sympatric populations (*ik-jk*) is used twice, once in the analysis for species *i* and once for species *j*. To adjust for this repetition we set α at 0.025, but we present all probabilities of <0.05. For the analysis of species *i* and *j* combined, each sympatric distance is used only once, but each allopatric distance (*ik-jm*) is sometimes used twice, once in comparison with the sympatric distance on island *k* (*ik-jk*) and once in comparison with the sympatric distance on island *m* (*im-jm*). This situation arises because congeneric species occur as often together on the same island as on separate islands. To adjust for this repetition, we serially deleted each allopatric distance once in each analysis and averaged the associated *P* values.

Results

Each Species Considered Separately

Table 2 gives the details and results of statistical tests. Nei's *D* between sympatric populations (*D*$_{sym}$) can be compared with the mean and range of allopatric populations of the same species (*D*$_{all}$). In 21 of the 26 comparisons, including all involving *Geospiza fuliginosa*, *D*$_{sym}$ is smaller than the average of allopatric *D* values. The next two columns in the table give the sample size of allopatric populations and the number of them for which *D*$_{sym}$ < *D*$_{all}$ in parentheses. The last three columns give the results of the two-tailed binomial tests of the null hypothesis that the number of comparisons where *D*$_{sym}$ < *D*$_{all}$ equals the number where *D*$_{sym}$ > *D*$_{all}$.

Figure 1 illustrates a strong tendency for ground finch species to be genetically more similar to each other in sympatry than in allopatry. In table 2, 18 of 52 tests (32.7%) provide statistical evidence of greater similarity in sympatry, and three give the opposite result at *P* < .05. In six cases, both species *i* and *j* are significantly more similar in sympatry than either is to any allopatric population of the other. These are *Geospiza magnirostris* and *Geospiza scandens* (*conirostris*) on Genovesa, *G. fuliginosa* and *Geospiza fortis* on Santa Cruz and Isabela, *G. fuliginosa* and *G. scandens* on Santa Cruz and San Cristóbal, and *G. fortis* and *G. magnirostris* on Santa Cruz.

In the aggregate, the high frequency of significant results in one direction is not expected by chance; 18 results in one tail of a normal frequency distribution and only three in the other has an associated two-tailed binomial probability of 0.002. Adjusting α to 0.025 to allow for the fact that the same genetic distance *ik-jk* between sympatric species is used in two tests reduces the ratio of significant differences from 18 : 3 to 14 : 1. The associated two-tailed binomial probability is 0.001. Also not expected by chance is the high frequency of low probability values (0.008); five of the 11 tests (about 45%) that could have produced such low values, because the sample size of eight was large enough, did so.

Table 2: Genetic distances of pairs of *Geospiza* species in sympatry (D_{sym}) compared with allopatry (D_{all})

Island of sympatry	*Geospiza* Species 1	Species 2	Sympatric D_{sym}	Allopatric mean D_{all}	Allopatric range D_{all}	N allopatric populations ($D_{sym} < D_{all}$) Species 1	Species 2	Probability[a] Species 1	Species 2	Combined species
Daphne	*magnirostris*	*scandens*	.550	.632	.515–.736	7 (5)	7 (7)	.016	…	.012
Santa Cruz	*magnirostris*	*scandens*	.562	.655	.515–.829	7 (7)	7 (6)	…	.016	.002
Rábida	*magnirostris*	*scandens*	.726	.694	.585–.948	7 (1)	7 (5)	…	…	…
Marchena	*magnirostris*	*scandens*	.841	.718	.567–.937	7 (1)	7 (0)	−.016	…	−.002
Genovesa	*magnirostris*	*scandens*	.484	.701	.538–.824	7 (7)	7 (7)	.016	.016	<.001
Daphne	*fuliginosa*	*fortis*	.230	.294	.172–.448	8 (8)	6 (2)	…	.008	…
Santa Cruz	*fuliginosa*	*fortis*	.131	.218	.134–.373	8 (8)	6 (6)	.032	.008	<.001
Santiago	*fuliginosa*	*fortis*	.216	.250	.134–.480	8 (5)	6 (3)	…	…	…
San Cristóbal	*fuliginosa*	*fortis*	.248	.268	.150–.515	8 (6)	6 (2)	…	…	…
Pinta	*fuliginosa*	*fortis*	.269	.333	.201–.515	8 (3)	6 (6)	.032	…	…
Isabela	*fuliginosa*	*fortis*	.143	.223	.145–.378	8 (8)	6 (6)	.032	.008	<.001
Daphne	*fuliginosa*	*scandens*	.510	.533	.316–.681	8 (2)	7 (7)	.016	…	…
Santa Cruz	*fuliginosa*	*scandens*	.312	.459	.316–.666	8 (8)	7 (7)	.016	.008	<.001
Santiago	*fuliginosa*	*scandens*	.565	.571	.425–.710	8 (6)	7 (2)	…	…	…
Rábida	*fuliginosa*	*scandens*	.555	.563	.403–.743	8 (3)	7 (4)	…	…	…
San Cristóbal	*fuliginosa*	*scandens*	.324	.459	.330–.700	8 (8)	7 (7)	.016	.008	<.001
Daphne	*fortis*	*scandens*	.529	.543	.339–.791	6 (0)	7 (7)	.016	−.032	…
Santa Cruz	*fortis*	*scandens*	.358	.445	.333–.581	6 (5)	7 (6)	…	…	.022
Santiago	*fortis*	*scandens*	.524	.570	.344–.684	6 (4)	7 (4)	…	…	…
Marchena	*fortis*	*scandens*	.685	.589	.416–.711	6 (1)	7 (1)	…	…	…
San Cristóbal	*fortis*	*scandens*	.434	.524	.333–.676	6 (5)	7 (5)	…	…	…
Daphne	*fortis*	*magnirostris*	.446	.350	.208–.518	6 (0)	7 (2)	…	−.032	−.022
Santa Cruz	*fortis*	*magnirostris*	.147	.251	.171–.370	6 (6)	7 (7)	.016	.032	<.001
Marchena	*fortis*	*magnirostris*	.238	.310	.176–.450	6 (4)	7 (6)	…	…	…
Pinta	*fortis*	*magnirostris*	.507	.418	.289–.534	6 (2)	7 (1)	…	…	…
Isabela	*fortis*	*magnirostris*	.250	.301	.171–.440	6 (5)	7 (4)	…	…	…

Note: Numbers of allopatric populations (N) for each species used in the comparisons with sympatric populations are given in columns 6 and 7, together with the number of comparisons (in parentheses) in which the genetic difference in sympatry (D_{sym}) is less than the allopatric difference (D_{all}). Probabilities associated with extreme frequencies of $D_{sym} < D_{all}$ are given in the last three columns, and a minus sign indicates extreme frequencies in the opposite direction $D_{sym} > D_{all}$. Ellipses indicate $P > .05$. The population of *Geospiza conirostris* on Genovesa has been included with *Geospiza scandens* owing to their close genetic similarity (Petren et al., forthcoming).

[a] Two-tailed binomial probabilities are shown for testing of the null hypothesis that the number of comparisons that yield $D_{sym} < D_{all}$ equals the number where $D_{sym} > D_{all}$.

Contrary to the general trend, the genetic distance between *G. scandens* and *G. magnirostris* on Marchena is very large when compared with allopatric populations of *G. scandens* (table 2). We have not studied the species on Marchena in detail. Possibly one or both species colonized it recently.

six probabilities <0.001 associated with the trend. Against the trend, the genetic distance between *G. fortis* and *G. magnirostris* on Daphne Major is large compared with allopatric distances. *Geospiza magnirostris* colonized Daphne in 1982–1983 and has not hybridized with any of the species (Grant et al. 2001).

Pairs of Sympatric Species Considered Together

Out of a total of 26 tests, nine pairs of populations (34.6%) are significantly more similar in sympatry than in allopatry, whereas two are significantly different in the opposite direction. In the aggregate, the associated two-tailed binomial probability of a 9 : 2 ratio approaches but does not reach statistical significance ($P = .066$). Noteworthy are

Tree Finches

Tree finches are not included in the above analyses for lack of adequate samples of populations of each pair of species for binomial tests; nevertheless, the few data are suggestive of similarity in sympatry in agreement with the hybridization hypothesis. For example, *Camarhynchus pauper* and *Camarhynchus parvulus* are believed to hy-
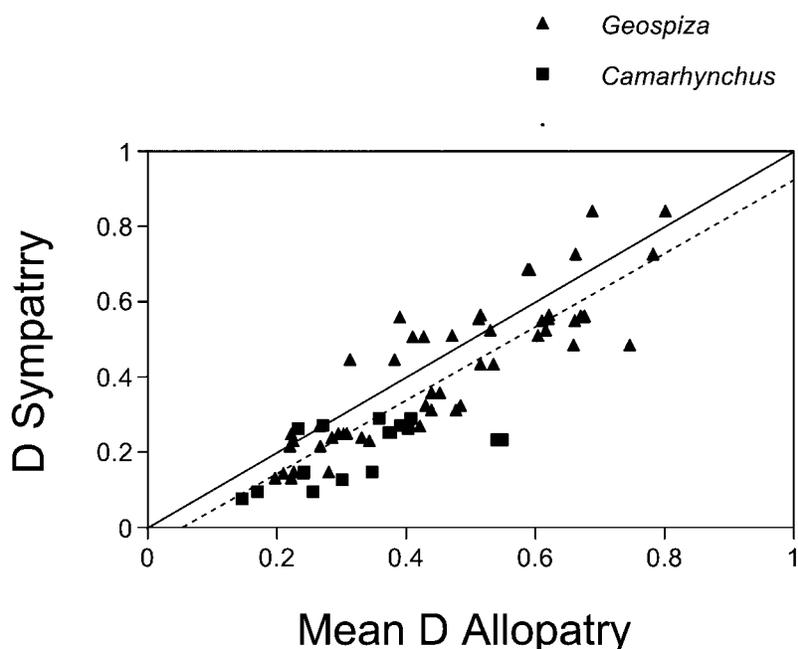
Figure 1: Closely related species of Darwin's finches are often genetically more similar to a sympatric relative than to allopatric populations of that relative. For each population of each species, the genetic distances with all allopatric populations of the other species have been averaged. Equality of sympatric and mean allopatric distances is shown by the solid line, and the trend line for all data calculated by ordinary least squares regression is shown as a dashed line. *Geospiza* are ground finch species, and *Camarhynchus* are tree finch species.

bridize on Floreana on the basis of museum specimens of intermediate morphology (Lack 1945, 1947). *Camarhynchus pauper*, occurring nowhere else in the archipelago, is more similar to sympatric *C. parvulus* ($D = 0.076$) than it is to two allopatric populations of *C. parvulus* ($D = 0.113–0.179$). *Camarhynchus psittacula* and *C. parvulus* may also hybridize (Lack 1945, 1947). These species are more similar to each other on Santa Cruz ($D = 0.095$) and Isabela ($D = 0.147$) than either is to five out of six allopatric populations of the other species ($D = 0.083–0.464$). To circumvent sample size limitations, we have combined all data for tree finches in the genus *Camarhynchus* in figure 1 and have compared all sympatric populations with the average of the heterospecific allopatric populations. In 15 out of 16 comparisons, the genetic distance between sympatric populations is shorter than the average distance from the allopatric populations. The two-tailed binomial probability of this result is <0.001. The same comparison of ground finch populations gives a 37 : 15 ratio in the same direction (large sample binomial test with correction for continuity: $z = 2.91$, $P = .0036$).

Discussion

We found a statistically strong tendency for a species to be more similar genetically to a sympatric relative than to allopatric populations of that relative. Genetic similarity of sympatric populations can be interpreted as evidence of a sympatric origin of species, evidence of introgressive hybridization, or both.

Sympatric Speciation

The logic of comparing sympatric and allopatric populations rests on the assumption of approximately constant rates of divergence in neutral alleles. Populations diverge in selectively neutral allele frequencies as a result of mutation and drift (assuming no selection on linked genes). Divergence is usually assumed to be stochastically time dependent, and the magnitude of independent change in the two lineages is assumed to be equal on average. However, allele frequency changes may occur faster early in the founding of a new population as a result of bottleneck effects on heterozygosity (Nei et al. 1975; Chakraborty and Nei 1977; Clegg et al. 2002; Grant 2002). If this happens, change will be greater in a lineage that has undergone several successive founder events in different environments (e.g., Clegg et al. 2002) than in a lineage that has remained in a single environment.

If species arise in a single location, and speciation occurs entirely sympatrically (e.g., Schliewen et al. 1994; Feder

1998; Via 2001), the sympatric populations are likely to be genetically more similar to each other at that location than are derived, bottleneck-affected populations whether they are sympatric or allopatric. However, introgression is an additional reason to expect genetic similarity because hybridization is most likely to occur early in the speciation history of two species (Grant and Grant 1997*a*).

One way to distinguish between these two causes of genetic similarity in sympatry is to use the fact that repeated patterns of genetic similarity in sympatry, in conjunction with differences between sympatric locations, are better explained by introgression than by any model of ancestral effects due to common ancestry or sympatric speciation (Matos and Schaal 2000; Shaw 2002). Thus, detecting genetic effects of introgression in a system where sympatric speciation occurs requires greater genetic similarity of species to be shown in at least two sympatric locations; if one is the location of origin, the other is a location of introgression since it is improbable that the same sympatric speciation would occur in two locations. In this study, we found two cases of members of a pair of species being most similar genetically in two sympatric locations. In two other instances, members of a pair of species were most similar genetically in one sympatric location. In these cases, sympatric speciation with bottleneck effects in derived populations could be a sufficient explanation. The populations in question are *Geospiza fortis* and *Geospiza magnirostris* on Santa Cruz and *G. magnirostris* and *Geospiza scandens* (*conirostris*) on Genovesa. Sympatric speciation has previously been invoked to explain an unusual distribution of beak sizes of *G. fortis* at the first location (Ford et al. 1973), although hybridization with *G. magnirostris* has been suspected (Grant 1999). Hybridization has been documented between the pair of species on Genovesa (Grant and Grant 1989).

Nevertheless, although some of the observations are consistent with a sympatric speciation explanation for the genetic similarities, there are two reasons to doubt that Darwin's finches have speciated in this way. The first is a general one. Sympatric speciation results from disruptive selection and genotype-dependent, perhaps frequency-dependent, mate choice (Arnegard and Kondrashov 2004; Seehausen and Schluter 2004; van Doorn et al. 2004). Given genetic variation in mate preference and genetic covariation with a preferred continuously varying trait, a species could diverge rapidly in the preferred and correlated traits (Kirkpatrick and Servedio 1999; Servedio 2000, 2004; Sætre et al. 2001; Servedio and Sætre 2003; Bolnick 2004). However, genetic variation in mate preferences is not known in birds (Bakker and Pomiankowski 1995), and if it exists, it is likely to be overwhelmed by uncorrelated environmental variation due to random effects and to learning. Like many other birds (Irwin and Price 1999; ten

Cate and Vos 1999), Darwin's finches imprint on morphological and vocal stimuli from their parents or other adults (Bowman 1983; Grant and Grant 1997*b*, 1998). Their songs are learned, culturally transmitted traits. Until a cultural equivalent to the sympatric speciation model of genetic variation and covariation is developed (see Lachlan and Slater 1999; Lachlan and Feldman 2003), the plausibility of sympatric speciation in songbirds remains doubtful except in unusual breeding systems (e.g., Payne et al. 2002; Sorenson et al. 2003).

More specifically, mate preferences have not been detected within species of Darwin's finches; mating appears to be generally random with respect to phenotype (Grant and Grant 1989, 1996, 1997*b*; Keller et al. 2001). The most favorable case for sympatric speciation involved a population of cactus finches *G. scandens* (*conirostris*) on Genovesa. In 1978, we found an ecological and morphological subdivision in the dry nonbreeding season (Grant and Grant 1979), possibly indicative of disruptive selection and incipient speciation; however, this was transitory because in subsequent wet seasons mating was not assortative (Grant and Grant 1987*b*), except for a tendency for experienced birds to pair together (Grant and Grant 1987*a*). Similar findings for some African finches have been reported by Smith (1993).

Coyne and Price (2000) reviewed the literature on island birds and found little evidence for sympatric speciation. We conclude that genetic similarity in sympatry is best accounted for by introgression.

Introgressive Hybridization

Genetic similarities of populations on Daphne and on Genovesa are congruent with long-term observations, although the situation on Daphne is complex. *Geospiza fortis* has hybridized with *Geospiza fuliginosa* and *G. scandens* there for at least the last 30 years (Grant et al. 2004). Although rare, interbreeding with *G. fuliginosa* predominated in the first half of that period (Grant 1993). The pattern of introgression changed in the second half when *G. fuliginosa*, never common, became rarer, and the frequency of interbreeding with *G. fortis* declined. Interbreeding of *G. fortis* and *G. scandens* increased, with genes flowing initially more from *G. scandens* to *G. fortis* and then later in the reverse direction. The net result was a genetic and morphological convergence of these two populations (fig. 2). *Geospiza scandens* underwent the largest change (Grant et al. 2004).

As expected from these observations, *G. fortis* is more similar genetically to *G. fuliginosa* and *G. scandens* on Daphne than to their respective allopatric populations (table 2). On the other hand, *G. scandens* differs genetically more from *G. fortis* on Daphne than from all allopatric
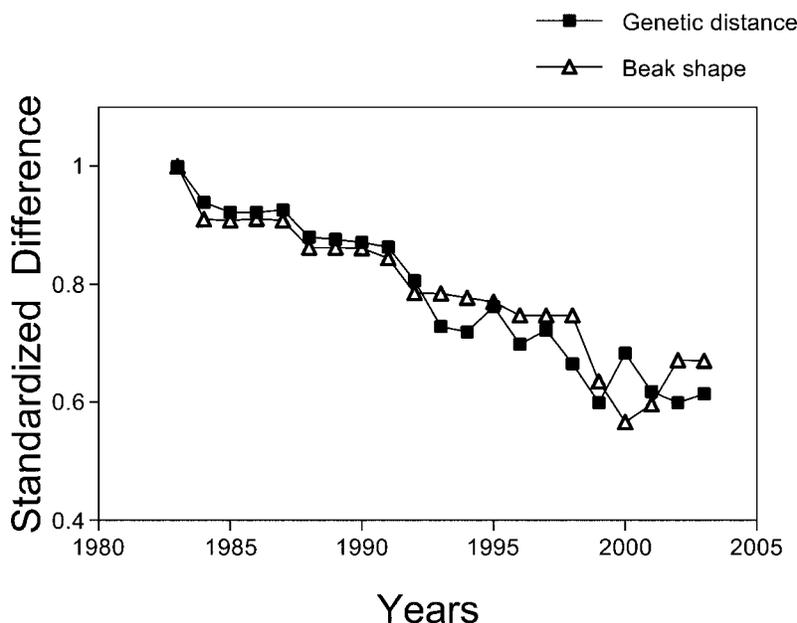
Figure 2: Morphological and genetic convergence of *Geospiza fortis* and *Geospiza scandens* on Daphne Major Island. Standardization was achieved by giving a value of 1.0 to the difference between the species in 1982 in beak shape and Nei's *D* (from Grant et al. 2004).

populations of *G. fortis*. We interpret this result to reflect a large effect of *G. fuliginosa* genes on *G. fortis* in the early part of the study. Data for table 2 were obtained before 1990; to be consistent with sampling on other islands, we included early samples preferentially. When the 2002–2003 samples are substituted for the earlier samples, the large genetic distance between *G. fortis* and *G. scandens* is greatly reduced (fig. 3). This demonstrates directly that the effect of introgressive hybridization is to diminish the genetic distance between sympatric species, both in absolute terms and relative to allopatric populations.

Despite providing strong support for the hypothesis, the method of comparing sympatric and allopatric populations is limited, as illustrated by a fourth species on Daphne, *G. magnirostris*. It colonized Daphne as a breeding species in 1982–1983 and since then has not hybridized with any of the resident species (Grant et al. 2001); yet, it is genetically more similar to Daphne *G. scandens* than to any other population of *G. scandens* (table 2), while at the same time it is substantially different from the sympatric population of *G. fortis*. The two most plausible explanations for these observations involve, first, the multiple origins of the *G. magnirostris* colonists (Grant et al. 2001) and, second, the particular pattern of genetic exchange among the other resident species as described above. This is a good example of how three-way or four-way interactions can complicate both the expectations and interpretations of two-way interaction data.

Introgression and Adaptive Radiation

The evidence for introgression is clearest with the most recently formed *Geospiza* species at the twigs of the phylogenetic tree, and it involves several populations. There is no reason to think introgression is solely a modern phenomenon. Therefore, we suggest that when older members were themselves at the twigs, they may have hybridized as often as modern species do and with the same evolutionary consequences. Indeed, there is indirect evidence that the basal warbler finch still hybridizes, though very rarely, with the more recently evolved tree finches (Bowman 1983; Grant 1999). Thus, introgressive hybridization may have been prevalent throughout the evolutionary history of finches on Galápagos. It could have facilitated evolutionary diversification of Darwin's finches and initiated speciation through the occasionally high proportion of hybrids and backcrosses by chance among the colonists of new small islands that have been repeatedly produced by fluctuating sea levels in the last million years or more (Grant 1999).

In other systems, introgressive hybridization is known to influence the speed and direction of evolution in new environments by elevating levels of genetic variation (Lewontin and Birch 1966; Chiba 1993; Wang and Szmidt 1995; Abbott et al. 2003), relaxing genetic covariation among traits (Grant and Grant 1994), and producing novel genotypes (Anderson and Stebbins 1954; Svärdson 1970;
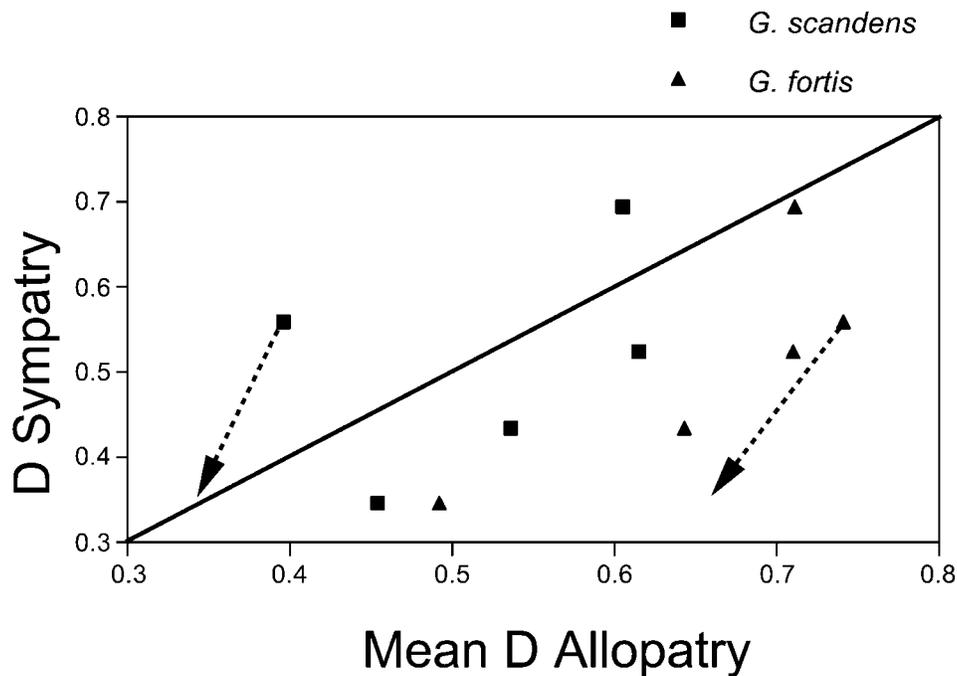
Figure 3: Effect of contemporary hybridization on genetic distances between *Geospiza scandens* and *Geospiza fortis*. Data are taken from figure 1. The effect of substituting samples from Daphne Major Island in 2002–2003 for pre-1990 samples is shown by dashed lines with arrowheads. The sympatric distance is greatly reduced as a result of persistent but rare introgressive hybridization. Additionally, this alters the mean allopatric distances by a small amount.

Rieseberg et al. 2003*b*). It potentially facilitates evolutionary divergence and speciation by refueling populations and reorienting their evolution when their environments change.

A stronger role for hybridization in the Darwin's finch radiation was first suggested by Lowe (1936), based on the botanical work of Lotsey (1916). He proposed that Darwin's finches represent a hybrid swarm, which can be defined as a population comprising "an extremely variable mixture of species, hybrids, backcrosses, and later generation recombination types" (Grant 1971, p. 155). A modified version of this idea has been independently applied to the finches by Seehausen (2004) and was used as a model for adaptive radiations in general. In this version, the radiation is not a hybrid swarm but is the product of diversifying selection on the elements of a swarm. For the scheme to work, markedly different species have to be produced first, and then hybridization creates a swarm. Evidence for the early occurrence of hybridization is a mismatch between nuclear and mitochondrial reconstructions of phylogeny at the base of a branch of diversification (Arnold 1992), owing to unequal exchange of nuclear and mitochondrial alleles (Shaw 2002). Depending on whether nuclear or mitochondrial genes introgress the most, one

set reflects phylogeny better than the other, and the other reflects superimposed effects of hybridization.

For example, the Cocos finch (*Pinaroloxias inornata*) is placed inconsistently on phylogenetic trees: at the base of the tree finch branch of the mtDNA tree (Sato et al. 1999; Burns et al. 2002) and at a much earlier point of origin on the microsatellite reconstruction (Petren et al. 1999). To account for this discrepancy, Seehausen (2004) proposed a hybrid origin of the tree and ground finches. However, this proposal necessitates a complex sequence of events involving dispersal of the Cocos finch from Galápagos to Cocos Island (600 km to the northeast) and divergence, followed by reversed dispersal to the Galápagos, interbreeding with a population related to the vegetarian finch (*Platyspiza crassirostris*), and eventual extinction on Galápagos. Alternatively, low levels of introgression could have affected microsatellite alleles but not mtDNA. This would have caused Galápagos species to converge genetically at nuclear loci, for which there is evidence, while the Cocos finch remained isolated and genetically distinct. Therefore, we doubt that hybridization was necessary for any part of the adaptive radiation of Darwin's finches as proposed under the hybrid swarm hypothesis, even though

the effectiveness of directional selection would have been aided by introgressive hybridization.

The hybrid swarm hypothesis may have more applicability to the cichlid fish of the African Great Lakes, where many more species evolved in a much shorter time (Kornfield and Smith 2000; Seehausen 2000; Danley and Kocher 2001; Allender et al. 2003; Kocher 2004). Increasing attention has been given to hybridization as a contributing cause (Salzburger et al. 2002; Smith et al. 2003; Schliewen and Klee 2004; Seehausen 2004). There are several more adaptive radiations (Schluter 2000) with unambiguous phylogenies that would be worth examining for evidence of lasting effects of hybridization. Distinguishing between hybrid speciation and introgressive influences on speciation is a challenge for future research to confront.

Acknowledgments

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