

Darwin's finches: Population variation and sympatric speciation

(Galapagos/song polymorphism/beak length/foraging differences/alternating territories)

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ABSTRACT The classical model of the adaptive radiation of Darwin's finches is one of repeated speciation in allopatry. Evidence presented here suggests that sympatric speciation may have contributed to the radiation. On Isla Genovesa *Geospiza conirostris* displays several features that are consistent with a model of sympatric speciation. Males are polymorphic in song type. Those singing song A have significantly longer bills than those singing song B. The two groups of males forage in different ways that are functionally associated with the bill differences, particularly in the nonbreeding season when food is probably limiting. Territories of mated song A and song B males alternate in space, whereas territories of unmated males do not. This suggests that females can discriminate between males on the basis of song and position, and the pattern is consistent with a hypothesis of assortative mating within song groups. The population is therefore polymorphic; the morphs occupy different niches in which they may be separately regulated and they could be on the way to achieving full reproductive isolation through assortative mating. It is suggested that the population may oscillate between fission and fusion tendencies due to a changing selection regime in this variable and unpredictable environment. There is no evidence that one of the morphs originated allopatrically and then immigrated to Genovesa. The possibility of sympatric speciation being partly responsible for the adaptive radiation, dismissed more than 30 years ago, should be reinstated.

Darwin's finches on the Galapagos and Cocos islands have contributed to the development of our understanding of evolution in general and of speciation in particular. Their diversity played an important part in stimulating Darwin to formulate the principle of natural selection (1). A century later that same diversity stimulated Stresemann to propose an explanation for the generation of several contemporary species from a single ancestral stock (2). Lack (3-5) elaborated the basic idea and proposed a model which has come to be known as the allopatric speciation model. The essential feature of the model is that a single species splits into two through the independent evolution of two or more populations on different islands; geographical isolation of the populations is a necessary condition for speciation. Generation of the 14 species of finches (subfamily Geospizinae) from a single ancestral species is explained as the result of repeated speciation events involving divergent evolution and adaptation to different ecological niches.

The allopatric model of the evolution of Darwin's finches was readily accepted and has since become a textbook example of what is regarded as the principal method of speciation in animals (6). Its widespread adoption has been due not to its originality, but to the clarity with which observations fit the theory.

The major alternative to this model is sympatric speciation. A single population splits into two, reproductively isolated, populations through divergent evolution of two segments; one becomes adapted to one set of ecological circumstances and the

other becomes adapted to another set. There is ecological isolation but no geographical isolation. Lack (5) raised this possibility with regard to Darwin's finches by suggesting that a population could become subdivided in two separate habitats. He then dismissed this by pointing out "two insuperable objections" (5). The first is the incompleteness of the isolation of the two subdivisions of the population. The second is the absence of any instances of birds known to be in the process of differentiating in adjoining habitats.

Lack's example of ecological isolation by habitat is a special case of sympatric speciation. Maynard Smith (7) has since proposed a general model of sympatric speciation. Genetic polymorphisms can give rise to separate species sympatrically if certain, rather stringent, criteria are satisfied: (i) the size of the polymorphic population is separately regulated in the two niches it occupies and the selective advantages of the morphs in their respective niches are large; and (ii) a mechanism causing reproductive isolation between the morphs, such as assortative mating, evolves.

We present evidence from a study of Darwin's finches that is consistent with the sympatric speciation model. Having done so, we discuss the difficulties of deciding which speciation model, allopatric or sympatric, best accounts for the facts.

Continuous and discontinuous variation

Natural selection may promote a large degree of genetic variation in populations living in heterogeneous environments (8). This is because individuals of different genotype are adapted to exploiting different parts of the environment. Support for this hypothesis has been obtained from our previous studies of Darwin's finches on the Galapagos Islands. Several populations of *Geospiza fortis* display a large phenotypic variation in bill dimensions, and within these populations different phenotypes are found in different habitat patches, exploiting foods of different size and hardness with efficiencies that can be correlated with their bill sizes (9). Because bill dimensions have high heritabilities (10), it is reasonable to assume that differences in phenotype reflect differences in genotype.

To find out if these results have general significance we studied another variable finch population, *G. conirostris* on Isla Genovesa (11). This island was chosen because it is low, flat, and isolated. There is no opportunity for adaptation along an altitude gradient and little opportunity for gene flow from other populations. We discovered an unusual variation. Adult male *G. conirostris* are segregated into two discrete phenotypes on the basis of song. Those males that sing one song type have significantly longer bills than males of the other song type, and these differences in bill size are associated with different feeding habits.

Song Variation. Nineteen breeding pairs of *G. conirostris* were observed in the period 19 January to 2 May 1978. Eight males sang a loud *ch ch ch*, which we designate song A, and the remaining eleven males sang a *chrrr*, which we refer to as song B (Fig. 1). In addition there were four unmated song A males

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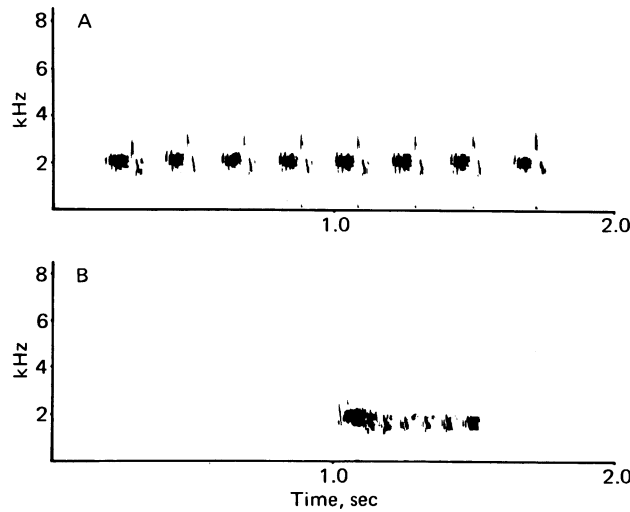


FIG. 1. Two types of song sung by male *G. conirostris* on Isla Genovesa.

and two unmated song B males. All males were in black plumage, which is an indication of reproductive maturity (11).

Song types are discrete. Tape recordings were made of songs produced by eight males of song A type and five males of song B type. The most conspicuous and consistent difference between the two song types is the rate of syllable production. It is more than twice as fast in type B (range 26–34/sec) as in type A songs (10–14/sec). A difference as consistent as this has a two-tailed probability of occurrence by chance alone of only 0.002 (Mann–Whitney *U* test). There are also differences in syllable structure between groups and a small variation in temporal patterning among type A songs. Song A corresponds to “basic” song and song B corresponds to “condensed” song in Bowman’s classification (12). Females did not sing.

All birds, except one song A pair, one song B pair, a female mated to a song B male, and two unmated song B males, were caught in mist nets, weighed, measured in standardized fashion (13), and given a unique combination of three-color bands and a numbered metal band before being released. It is from subsequent observations of these banded birds over periods of up to 4 months that we know each individual male sings only one song type.

Morphological Variation. Comparisons of song A and song B males show a significant difference in bill length but not in any other dimension (Table 1). The average bill length of song B males is 6.3% smaller than the average for song A males. A consequence of the difference in means is that the variation of

Table 1. Weight and dimensions of *G. conirostris* on Isla Genovesa, separated into two groups on the basis of song type

Morphological character	Type A (<i>n</i> = 11)	Type B (<i>n</i> = 10)	Test for differences between groups	
			<i>t</i> ₁₉	<i>P</i>
Weight, g	25.85 ± 0.52	24.96 ± 0.73	1.01	>0.1
Wing length, mm	78.3 ± 0.7	77.7 ± 0.6	0.62	>0.1
Tarsus length, mm	22.67 ± 0.23	22.33 ± 0.21	1.08	>0.1
Bill length, mm	15.47 ± 0.14	14.55 ± 0.20	3.87	<0.002
Bill depth, mm	10.79 ± 0.18	11.02 ± 0.36	0.58	>0.1
Bill width, mm	9.99 ± 0.45	10.23 ± 0.23	0.89	>0.1

Means and one standard error are shown; *n* = sample size.

the combined group of males is greater than the variation of each; the coefficient of variation for the combined group is 5.47, whereas for the song A and song B groups treated separately it is 2.96 and 4.31, respectively. The value of 5.47 for the combined group is remarkably similar to the value of 5.37 calculated from measurements of museum specimens (11).

Females paired with song A and song B males did not differ significantly from each other in any measured dimension (*P* > 0.1 in each case). There may be a real but small difference in bill length between the two groups of females in parallel with the difference between the males. If so, our sample sizes are insufficient to detect it. Females paired with song B males did not differ from those males. However, females paired with song A males have shorter bills than song A males (*t*₁₅ = 2.34, *P* < 0.05). Thus, song A males have longer bills than both their females and song B males.

Ecological Variation. The types of food and the times spent feeding by identified individuals were recorded. Observations on foraging were made between 0700 and 1000 during 11 5-day periods between 25 January and 30 April. The same areas were searched during each sampling period with approximately equal intensity. To minimize possible biases arising from an over-representation of conspicuous individuals in our records, we set an upper limit of 300 sec of foraging activity per bird per day. Theoretically this could allow a maximum of 1500 sec per bird per 5-day period; but in fact only two birds were recorded feeding as much as 300 sec in any one activity during a period. The only instance of an individual dominating a foraging activity is in bark stripping. Where there was a difference between bird groups in number of seconds devoted to a foraging activity, there was generally a difference in the same direction in the number of birds involved in that activity. One of us (P.R.G.) returned to the island in the nonbreeding season and made further observations on foraging in the period 10–26 November, in the same manner as previously.

Foraging differences are associated with bill length differences between the two groups of males (Table 2). In the breeding season (January to April) the long-billed song A males spent more time feeding on *Opuntia* (cactus) flowers, whereas song B males with shorter bills spent more time feeding on the ground and tearing at *Opuntia* pads to reach moist pulp, insect larvae, and pupae. To test for a difference in the frequency of foraging activities we multiplied the number of birds observed in an activity by the number of periods in which each was observed to engage in that activity. There are 32 bird-period records of song A males feeding on *Opuntia* flowers and 16 such records for song B males. For *Opuntia* pad ripping there are 0 and 6 records, respectively. The difference in proportions between the two groups of males is significant; Fisher’s exact test, two-tailed *P* = 0.006.

Table 2. Proportion of time spent foraging in various ways by adult male *G. conirostris* on Isla Genovesa, Galapagos

Foraging activity	Jan.–April		November	
	Type A	Type B	Type A	Type B
Gleaning	0.272	0.251	—	—
Bark stripping (<i>Bursera</i> , <i>Croton</i>)	0.106	0.014	0.154	0.110
<i>Opuntia</i> pad ripping	—	0.120	—	0.463
Pecking on ground	0.081	0.219	—	—
Fruits on <i>Croton</i>	0.052	0.099	—	—
Fruits on <i>Bursera</i>	0.258	0.172	—	—
Flowers and buds on <i>Opuntia</i>	0.231	0.124	0.356	0.426
Fruits on <i>Opuntia</i>	—	—	0.390	—
Total time, sec	6537	4892	2435	1630

In the nonbreeding season the foraging differences between the two groups of males are more striking and center almost entirely on how the birds exploit *Opuntia* cactus (Table 2). Both groups feed on flowers and buds (eight individuals observed), but only song A males (five of them) were observed to feed from fruits on *Opuntia* bushes by drilling a hole in the fruit with the bill and eating the pulp from around each seed and only song B males (six) were observed ripping open *Opuntia* pads and feeding on the pulp. The numbers of birds engaging in these three ways of exploiting *Opuntia* were used to test the hypothesis that the two groups of males used the three activities with equal frequency. This hypothesis was rejected; $\chi^2_2 = 11.48$, $P < 0.005$.

These results suggest that the bill difference between the two groups of males is functionally related to the foraging differences because a long bill is advantageous in probing and a short and relatively stout bill is advantageous in crushing or tearing large and hard food items (11, 14). One expects the significance of a difference in bill size to be more apparent in the nonbreeding season, when food supply is lower and the regulation of numbers is likely to occur, than in the breeding season when food is abundant (15). This is indeed what we observe with the two groups of male *G. conirostris*.

There are fewer data for females. In both seasons there were no significant differences in foraging between the two groups of females or between either female group and their respective male groups. Thus, the major difference in bill size and foraging characteristics lies with the two groups of males.

Genetic Variation. Sexual dimorphism in average bill size is a common phenomenon in some groups of birds (16), but a dimorphism in average bill size between adult members of one sex that differ in song type has not been reported for any species. The question arises, are these two song groups genetically different? It is reasonable to assume that they are in view of the high heritability of bill size in the closely related congener *G. fortis* (10). There is further evidence of a genetic difference between the two song groups from nestling bill color. Nestling bill color is dimorphic; bills are either pink or yellow. The frequency of yellow morphs in nestlings of the song A males (36%; n nestlings = 59) is twice as high as in the nestlings of song B males (18%; n = 79). The difference is significant ($\chi^2_1 = 5.70$, $P < 0.02$). Although we have no direct evidence, we believe the color variation to be under genetic control because it appears at hatching before the nestlings have been fed by their parents. Furthermore, the frequencies of the morphs differ among the three *Geospiza* species on Isla Genovesa (*G. conirostris*, *magnirostris*, and *difficilis*) even though diets are similar in the breeding season (unpublished observations).

Separate regulation in two niches

The first condition of Maynard Smith's sympatric speciation model is similar to the Van Valen hypothesis (8) for the maintenance of large morphological variation in a heterogeneous environment. Our results are consistent with this hypothesis. We have demonstrated a feeding niche difference between the two groups of males during the breeding season, and also during the nonbreeding season when food is likely to be limiting (15). The possibility that the numbers of the two groups are separately regulated is made plausible by analogy with different species. A variety of studies has shown that sympatric congeneric species of birds, however similar in appearance, have different feeding niches (17–21). From these observations it is generally assumed that the species owe their sustained coexistence to regulation by different food factors (22). If species are separately regulated, different morphs within a species may also be separately regulated providing the foraging differences

between morphs are equivalent to foraging differences between species. This provision is close to being satisfied on Isla Genovesa.

We made feeding observations during our study on *G. magnirostris*, a congener sympatric with *G. conirostris*. In the nonbreeding season the foraging activity of male *G. conirostris* and male *G. magnirostris* scarcely overlapped; using Whitaker's index (23) we calculate a similarity of 0.12 (on a scale of 0–1; see also ref. 15). At this time the similarity between song A and song B male *G. conirostris* was 0.50. However, this relatively high value was due mostly to *Opuntia* flowers and buds, which only start to appear in late October. Prior to this time food is likely to be scarcer. If the two groups of *G. conirostris* males fed in early October as they did in November, except for the omission of *Opuntia* flowers, their similarity would be 0.19, and hence close to the above interspecific value. Although based on estimation and not observation, this is enough to show a potential separate regulation of the two male groups by different food factors. These food factors are part of a single plant species and therefore might be considered a single factor instead, but there is no necessary proportional relationship between the two. Moreover there are theoretical reasons for believing that different plant parts can act to regulate different populations of exploiters (24).

Reproductive isolation

The second condition is a mechanism for reproductive isolation. Theoretically, reproductive isolation of the song groups could occur through assortative mating as a result of imprinting (25) of the young on male parent's song. Although we have as yet no direct evidence of imprinting upon father's song in *G. conirostris*, Bowman (12) has evidence of imprinting in other geospizines from both field and laboratory studies. Our study provides indirect evidence of assortative mating on the basis of song. The evidence is from the distribution of territories in the breeding season.

Territories of song A and song B males alternate in such a way that no two breeding males of the same song type shared a territory boundary (Fig. 2). There were 11 boundaries between territories owned by breeding males of unlike song type and none between territories owned by breeding males of the same song type. The ratio of 11:0 differs significantly from the equal frequencies expected from a hypothesis of random distribution of territories of the two male groups with respect to each other

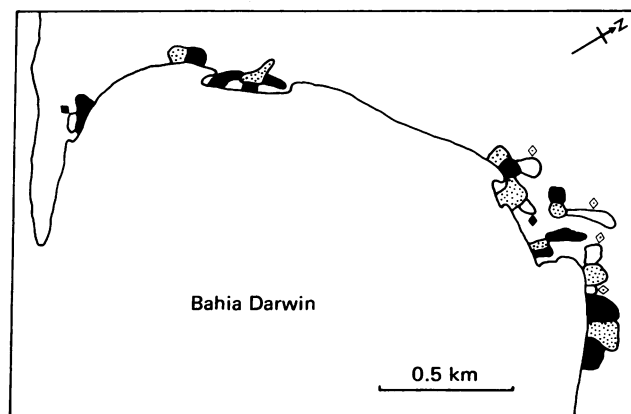


FIG. 2. Territories of *G. conirostris* on Isla Genovesa. Solid areas depict territories of mated song B males; stippled areas show territories of mated song A males. Open areas indicate territories of unmated males, either of song A (◇) or song B (◆) type. There were no *G. conirostris* territories on areas left blank or around the eastern half of B. Darwin because those lacked cactus (*Opuntia*) or had sparse cactus growth.

(two-tailed binomial test, $P < 0.002$). In contrast to this result, boundaries between an unmated male's territory and the territory of another unmated male or of a mated male gave a ratio of 3:4. This is in agreement with the null hypothesis but differs significantly from the ratio for mated males (Fisher's exact test, $P = 0.023$).

These patterns might be explained by supposing the two types of males select different types of vegetation in which to nest and hold territories. Feeding is almost confined to the territories in the breeding season, but is less restricted in the nonbreeding season. We made rough estimates of the abundance in each territory of the five major plant species and their reproductive products: *Opuntia helleri*, *Bursera graveolens*, *Croton scouleri*, *Cordia lutea*, and *Waltheria ovata*. We found no differences in size or floristic composition of territories of the two song groups, nor was there a difference in nest placement; 38 of 40 nests (groups combined) were in *Opuntia*. These results show, incidentally, that the polymorphism is not maintained by one mechanism envisaged by Maynard Smith (7), females nesting in the "niche" in which they were raised.

We do not know how these patterns of territories are created because the territories were already established when our study began and all but three of the breeding males (two song A and one song B male) already had mates. Nevertheless, if pairing generally takes place during or after the establishment of territories, some interesting inferences can be made. The differences in pattern of distribution of territories between mated and unmated males implies that females choose mates on the basis of position and could thereby select for a differential responsiveness by males to song type. On several occasions countersinging was heard between males of like song type, even when separated by a territory occupied by a mate of unlike song type. Countersinging between males of unlike song type was not heard. Unfortunately, we did not quantify song production. More importantly, the difference in pattern of distribution of territories between mated and unmated males also implies that females are sensitive to, and respond to, the differences between male songs. The results are consistent with the hypothesis of assortative mating by song type.

Choice between models

In spite of this consistency, there are two difficulties in applying the sympatric speciation model to this situation. The first concerns the likelihood that the speciation process goes to completion. Gene exchange between the two song groups will arrest or retard the process to a degree dependent upon several factors, including the amount of gene exchange (26, 27, 28). Here our understanding is uncertain, both in theory and in practice.

According to one model (25), absolute assortative mating is essential for the process to go to completion—i.e., matings are always homotypic. Absolute assortative mating implies that birds of either sex elect not to breed if there is no available mate of the right song group. We think that it is more likely that birds prefer to mate within their song group, but if there are difficulties in finding a mate of the right type a member of the other group will be accepted. The supply of mates is likely to vary from year to year in this unpredictable environment because the population of *G. conirostris* apparently experiences extreme fluctuations in size (29). Occasional heterotypic matings would create new genetic combinations in the population. This might be responsible for the population retaining a large variation in spite of frequent drops in numbers and the danger of losing alleles through random drift. Therefore, the genetic structure of the population can be thought of as fluctuating between two opposing processes, subdivision through imprinting and assortative mating and fusion through random mating.

To test this idea we need information on the matings of birds of known paternal song type. Our study cannot supply this information. Of 120 banded nestlings of known paternal song, only one was found in November. If other populations are polymorphic in songs, it may be possible to investigate mating patterns with them. Assortative mating with respect to beak size has been demonstrated in the *G. fortis* population on Isla Daphne (10).

The second difficulty concerns the origin of the song polymorphism. Although Genovesa is well isolated, one of the song morphs may have originated on another island and immigrated to Genovesa. We can find no evidence for this. The only other *G. conirostris* populations occur on Isla Española and Isla Gardner at nearly the furthest point in the archipelago from Genovesa. Songs are complex and like neither song type on Genovesa. This may be contrasted with a somewhat similar situation on Isla Santa Cruz. Ford *et al.* (30) found a bimodal tendency in the frequency distribution of beak sizes in male *G. fortis* at a site on the southern side of the island. They suggested the population may be splitting into two species under disruptive selection. The area is known to be floristically diverse (14). However, the bimodality can also be explained by recent invasion of differentiated *G. fortis* from Isla San Cristóbal, an island to the south of Santa Cruz, and with a tendency for each of the original and recent stocks to breed assortatively (9). Here a potential source of immigrants can be identified by their unusual properties. For *G. conirostris*, a source cannot be identified.

G. conirostris on Genovesa represents a stage in the process of speciation. The facts are consistent with both an allopatric and sympatric model. Unless one is willing to claim parsimony for the sympatric model (31)—no interisland dispersal and differentiation in allopatry required—it seems best to recognize that the data are insufficient to discriminate between them.

These difficulties pervade all arguments over sympatric speciation (6, 31–35). Our study does not help to resolve those arguments. It does suggest that the adaptive radiation of Darwin's finches may not have been produced exclusively by repeated speciations in allopatry (see also ref. 30), that at the very least sympatric speciation cannot be dismissed as was done more than 30 years ago (5). This is of general significance because other plausible examples of "gradual" sympatric speciation have come from plants and insects, not from vertebrates (35). Finally, it provides strong support for the hypothesis that natural selection maintains variation in a heterogeneous environment (8). The frequencies of the two song morphs in the *G. conirostris* population are too high to be accounted for by immigration or mutation, so local factors must be responsible for their maintenance; and, as Maynard Smith (7) has stressed, the establishment of a stable polymorphism in a heterogeneous environment is a crucial step in sympatric speciation.

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