

HYBRID SPECIATION

Rapid hybrid speciation in Darwin's finches

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Homoploid hybrid speciation in animals has been inferred frequently from patterns of variation, but few examples have withstood critical scrutiny. Here we report a directly documented example, from its origin to reproductive isolation. An immigrant Darwin's finch to Daphne Major in the Galápagos archipelago initiated a new genetic lineage by breeding with a resident finch (*Geospiza fortis*). Genome sequencing of the immigrant identified it as a *G. conirostris* male that originated on Española >100 kilometers from Daphne Major. From the second generation onward, the lineage bred endogamously and, despite intense inbreeding, was ecologically successful and showed transgressive segregation of bill morphology. This example shows that reproductive isolation, which typically develops over hundreds of generations, can be established in only three.

Interbreeding of two species may result in the formation of a new species, reproductively isolated from the parental species (1). Hybrid speciation without chromosomal doubling, that is, homoploid hybrid speciation, is rare (1–4). Possible examples have been reported in plants (4), butterflies (5), flies (6), fish (7), mammals (8), and birds (9). However, only one of these, involving *Heliconius* butterflies (5), and three additional examples, involving *Helianthus* sunflowers (3, 10), meet stringent criteria that have been proposed for recognizing that hybridization was the cause of speciation (2). Here we report the results of a combined ecological and genomic study of Darwin's finches that documents hybrid speciation in the wild from its inception to the development of reproductive isolation.

An immature male finch immigrated to the small Galápagos Island of Daphne Major (0.34 km²) in 1981 (11–13). It resembled the medium ground finch *Geospiza fortis*, but was 70% larger and sang a distinctive song. Assignment tests with microsatellite markers from finches on neighboring islands indicated that it was possibly a *G. fortis* × *G. scandens* hybrid originating on the adjacent large island of Santa Cruz, 8 km from Daphne (11). We followed the survival and breeding of this individual and its descendants for six generations over the next 31 years.

The immigrant (generation 0) bred with a *G. fortis* female and one of its F₁ offspring bred with another *G. fortis* female, but all other matings occurred within this lineage, endogamously; therefore, from generation 2 onward, the lineage be-

haved as an independent species relative to other birds on the island (Fig. 1). Generations 4 to 6 were derived from a single brother-sister mating in generation 3. Despite close inbreeding, members of the lineage experienced high fitness, as judged by their reproductive output and high survival (12). At maximum (in 2010), eight breeding pairs and 36 individuals were present on the island, and on our most recent visit (in 2012), there were eight breeding pairs and 23 individuals of generations 3 to 6. From observations and experiments with ground finches (12, 13), bill morphology is likely to be a key factor in the success of these birds. The ability of finches to efficiently exploit the large woody fruits of *Tribulus cistoides* in dry seasons, and particularly during droughts and limited food supply, is a function of bill size, especially bill depth (12). Also, finch species imprint on features of their parents early in life, and later, when choosing a mate, they discriminate between members of their own and other species on the basis of bill size and shape, as well as body size and song (13).

We combined morphological measurements and whole genome sequencing of almost all individuals in the new lineage to establish the genetic basis of the founder population and characteristics associated with its success. We (i) assigned the founder male to species and source population, (ii) confirmed pedigree assignments from observations and sequence data (14), (iii) quantified patterns of gene transmission between generations, (iv) assessed genetic diversity, and (v) searched for genetic clues to the success of the lineage.

Because members of the new lineage are conspicuously large, we refer to it as the Big Bird lineage (12).

A phylogenetic tree analysis showed that the founder male (individual 5110) was not a *G. fortis* × *G. scandens* hybrid as previously hypothesized (12), but rather a *G. conirostris* (Fig. 2A). This species (large cactus finch) occurs on Española and its satellite Gardner (Fig. 2B) and nowhere else in the Galápagos archipelago; a population on Genovesa, formerly classified as *G. conirostris*, was recently reclassified as *G. propinqua* (15). Immigration from Española is noteworthy and unexpected because it is located more than 100 km from Daphne Major and a large island (Santa Cruz) lies between them (Fig. 2B). Rare long-distance movements of finches in the archipelago have been detected before, but, until recently, it was assumed these birds were vagrants that did not stay to breed (16–18).

The founder had an inbreeding coefficient (*F*) of 0.19 and appeared to be a typical member of the source population of *G. conirostris* from Española (*F* = −0.04 to 0.31), in terms of average genome-wide homozygosity, and admixture (19) analysis classified it as a normal *G. conirostris* (Fig. 2C). The inbreeding coefficient was negative in the F₁ generation (Fig. 2D) as a result of the interspecies hybridization (12, 13). A gradual increase in homozygosity was then observed over the next five generations (Fig. 2D), as expected from the small number of breeding pairs (one to eight), causing genetic drift. Genome-wide average nucleotide diversity π showed a similar

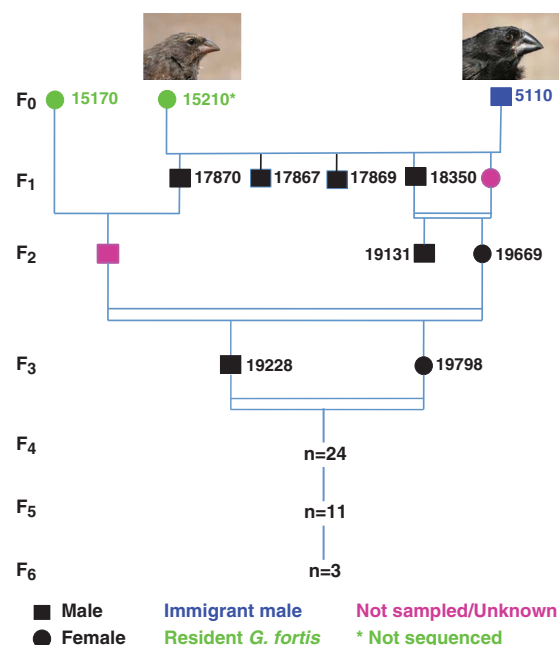


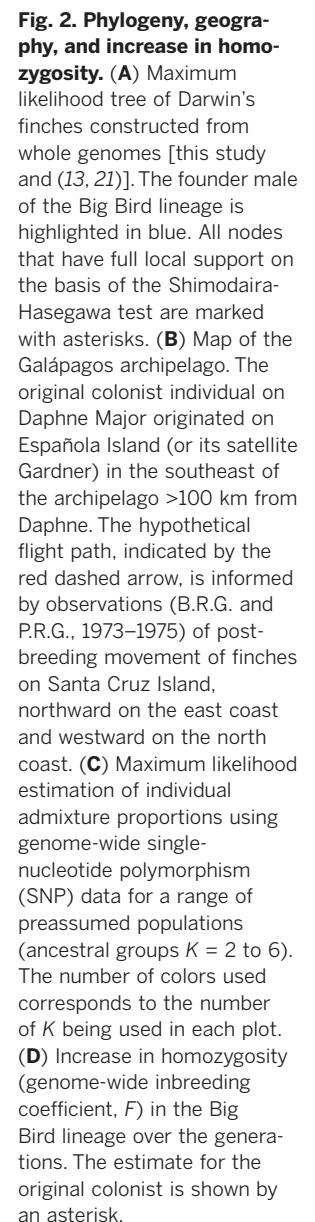
Fig. 1. The Big Bird lineage through the sixth generation.

Interbreeding with two *G. fortis* females resulted in a reduction of the genetic contribution of the immigrant male from 0.50 in the first generation to 0.375 in the second and subsequent generations. The numbers indicate identification number (14). *n* indicates number of individuals. [Photo credit: Peter and Rosemary Grant]

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The ecological success and reproductive isolation of the Big Bird lineage were most likely due to large bill and body size and a distinctive song (12). We undertook a more detailed morphological analysis of the new lineage, together with both of the parental species *G. conirostris* and *G. fortis* [(14), table S1]. In body size, the members of the Big Bird lineage are intermediate, on average, between the means of the parental species