



## 50 Years Ago

Recent investigations have shown that the fluoride content of Greek teeth from the cities of Athens and Salonika was considerably high. This may explain, at least in part, the low prevalence of dental caries observed in Greece ... With the exception of sea salt, however, the fluoride content of other foods commonly produced and consumed in Greece is not known ... The analyses showed that the fluoride content of olive oil from the Island of Crete was 0.36 p.p.m. and that from the area of Kalamai 0.63 p.p.m. ... it appears that the inclusion of olive oil in the daily Greek diet does not make any significant contribution to the amount of ingested fluoride. Thus, at present, sea salt remains an important source of dietary fluoride in Greece for protection against dental caries. This may well be the case in other countries, such as Taiwan, Ceylon and Lebanon, where because of local food customs the amount of sea salt consumed has been estimated to be considerable: about 16–20 g per person per day.  
From *Nature* 14 March 1964

## 100 Years Ago

Think of the Niagaras of speech pouring silently through the New York telephone exchanges where they are sorted out, given a new direction, and delivered audibly perhaps a thousand miles away. New York has 450,000 instruments — twice the number of those in London. Los Angeles has a telephone to every four inhabitants ... Our whole social structure has been reorganised. We have been brought together in a single parlour for conversation and to conduct affairs, because the American Telephone and Telegraph company spends annually for research ... a sum greater than the total income of many universities.  
From *Nature* 12 March 1914

Initial experiments to address these questions have failed to provide clear answers. Coen *et al.* show that song transitions are similar whether or not the singer is ultimately successful in mating. Yet pheromone-insensitive males, who sing for normal durations but have altered song patterning<sup>8</sup>, tend to be slower and less successful in convincing females to mate<sup>1,8</sup>. Whether these flies are handicapped in the courting game because of a defect in how they vary their songs, or because of unrelated effects, remains to be seen. But whether song patterning matters to females or not, we now know that its variability, and probably the variability of many other ‘fixed’ behaviours, is not simply the consequence of noise in nervous-system function<sup>6,7</sup>. Rather, a sizeable fraction of that variability is likely to reflect computations performed by reliable and predictable brains on an ever-changing sensory environment.

Importantly, this insight was made possible by simultaneously observing, at high temporal resolution, the sensory environment and behavioural output of a genetically tractable organism during a complex social interaction. Such detailed analysis applied to natural behaviours has the power, as Coen *et al.* aptly demonstrate, to distil seemingly complex and unpredictable behavioural patterns into simple rules and sensorimotor transformations<sup>9,10</sup>. With such an

approach, rather than being the fog that prevents us from understanding nervous-system function, behavioural variability and complexity can be the searchlight that helps us to identify the computational problems that brains evolved to solve. ■

**Bence P. Ölveczky** is in the Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138, USA.  
e-mail: olveczky@fas.harvard.edu

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### EVOLUTIONARY BIOLOGY

# Speciation undone

**Hybridization can cause two species to fuse into a single population. New observations suggest that two species of Darwin’s finches are hybridizing on a Galapagos island, and that a third one has disappeared through interbreeding.**

PETER R. GRANT & B. ROSEMARY GRANT

The process of speciation, in which one species splits into two, is vulnerable to collapse in its early stages through interbreeding and the exchange of genes, a process referred to as introgression. As explained by the evolutionary biologist Theodosius Dobzhansky<sup>1</sup>, “Introgressive hybridization may, then, be a passing stage in the process of species formation. On the other hand, the adaptive value of hybrids may be as high as that of their parent; introgressive hybridization may lead to obliteration of the differences between the incipient species and their fusion into a single variable one, thus undoing the result of the previous divergent development.” Writing in *American Naturalist*, Kleindorfer *et al.*<sup>2</sup> offer a possible example of this process, in a study suggesting that one population of Darwin’s finches has become extinct through interbreeding with another.

Until Kleindorfer and colleagues’ report, three species of tree finch were known to occur together in the highlands of Floreana Island in the Galapagos (Fig. 1). They differ in body size and in the size and shape of the beak, but, unlike many birds elsewhere, not in plumage. The medium tree finch (*Camarhynchus pauper*) is present only on Floreana, whereas the small tree finch (*Camarhynchus parvulus*) and large tree finch (*Camarhynchus psittacula*) also occur together on several other islands. The pattern of distribution and size differences led evolutionary biologist David Lack to suggest<sup>3</sup> that speciation had occurred on Floreana through the invasion of large tree finches from Isabela Island, followed by evolutionary reduction in average size. The resulting medium tree finches did not interbreed with the large tree finches that arrived later, apparently from Santa Cruz Island.

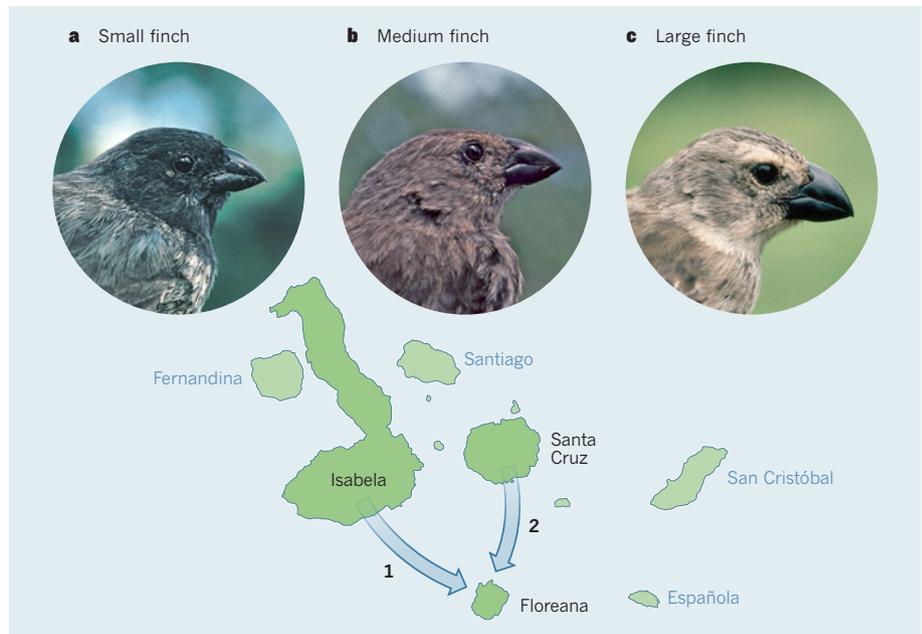
Kleindorfer and colleagues now report that this pattern no longer exists: the large tree finch

has disappeared from Floreana! By comparing the morphological features of present-day Floreana finches (studied in 2005 and 2010) with historical data, and conducting a genetic study of current populations using DNA-sequence markers (microsatellites), the authors show that there are currently only two distinct populations on the island, corresponding to the small and medium tree finches. The analyses also revealed that individuals that do not fit into either population show intermediate characteristics, suggesting that they are hybrids. Consistent with the hypothesis of ongoing hybridization on the island, the authors observed females of the morphologically larger group (the medium tree finch) pairing with males of the smaller group, and they identified 15% of yearling males in 2010 as hybrids.

The authors suggest that hybridization may have been responsible for the disappearance of the large tree finch from Floreana, and that it may now be causing the remaining two species to fuse into one: speciation in reverse<sup>4</sup>. What has brought this about? The most likely answer is anthropogenic change to the habitat. A human settlement was established on the island just before Darwin's visit in 1835. The natural vegetation subsequently became rapidly degraded, and by the end of the nineteenth century two species of finch and a species of mockingbird had become extinct<sup>5</sup>. The large tree finch was rare: only 4 male and 13 female specimens were collected for museums between 1852 and 1906. The birds may have experienced difficulty in finding mates of their own species, hybridized with medium ground finches and become absorbed into the population<sup>2,5</sup>.

Alternatively, the large tree finch may have become extinct through changes in the food supply alone, without any interbreeding. One way of distinguishing between the two hypotheses might be to use molecular markers to search for evidence of past introgression. If markers could be identified in the genomes of large tree finches on Santa Cruz (and the museum specimens from Floreana) but not on Isabela, and also found in the medium tree finches, they could be the smoking gun of introgression.

To identify hybrids between the remaining medium and small tree finches, Kleindorfer *et al.* relied on a clustering technique with (acknowledged) low statistical power. But two other identifying clues are at hand. The first is beak shape, which is known to be a marker of species identity in these finches<sup>3,5</sup>. The second is song. Different species of Darwin's finches sing different songs, which are acquired through learning by nestlings and fledglings and used by adults to identify mates<sup>6,7</sup>. A song of a large tree finch was tape-recorded on Floreana in January 1962<sup>6</sup>, but we failed to see or hear any of these birds on five visits during 1979–2004<sup>8</sup>. The song of a large tree finch coming from the mouth of a medium tree finch could be a



**Figure 1 | Invasion, evolution and loss.** Three species of Darwin's finches, the small tree finch *Camarhynchus parvulus* (a), the medium tree finch *Camarhynchus pauper* (b) and the large tree finch *Camarhynchus psittacula* (c), have been known to inhabit the Galapagos island of Floreana. The medium finch occurs nowhere else in the archipelago, and its morphological distinctiveness was interpreted by evolutionary biologist David Lack to be the result of invasion of a small form of *C. psittacula* from Isabela (1), followed by an evolutionary reduction in size and change in beak shape<sup>3,5</sup>. Later, a larger form of *C. psittacula* invaded from Santa Cruz (2), and remained unchanged. However, Kleindorfer *et al.*<sup>2</sup> now report that this large species is no longer found on Floreana.

wail from the ghost of an interbreeding past.

Although there is some uncertainty about hybrid identification in this study, the disappearance of a species through hybridization is certainly plausible. On the small uninhabited island of Daphne Major, two species of ground finch (genus *Geospiza*) have been converging morphologically and genetically for more than 30 years as a result of persistent (although rare) introgressive hybridization following a natural change in the food supply. If introgression continues at the same rate, the two species will fuse into one in approximately 40 years<sup>7</sup>. The finches of Daphne Major are also a reminder that, under special circumstances, hybridization can lead to the opposite outcome — the formation of a new species. A new genetic lineage has become established on Daphne by an immigrant hybrid from Santa Cruz, and is now behaving as a separate species (see ref. 7 for further details).

Kleindorfer and colleagues' findings suggest that the small and medium tree finches on Floreana may also be fusing into one species. The authors raise the intriguing possibility that hybrids between these populations have an immunological advantage over the parental species in the face of attack by a parasitic fly, *Philornis downsi*, whose larvae eat and kill finch nestlings. The fly was introduced to the archipelago 50 years ago<sup>9</sup>. Their study is important because it adds weight to a growing concern that we humans are causing loss of biodiversity by altering habitats, in some cases by bringing separate species into proximity and causing

their extinction through interbreeding<sup>10,11</sup>. Rapid radiations of fishes<sup>11,12</sup> and finches<sup>5</sup> are especially at risk because their morphological evolution is not accompanied by strong barriers to gene exchange. Uniquely valuable in showing how speciation is done<sup>7,13</sup>, such species deserve special protection from being artificially undone. ■

**Peter R. Grant and B. Rosemary Grant** are in the Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08540, USA. e-mails: [prgrant@princeton.edu](mailto:prgrant@princeton.edu); [rgrant@princeton.edu](mailto:rgrant@princeton.edu)

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