



Evolution of the Atlantic-island Chaffinches

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Common Chaffinch *Fringilla coelebs*, Canaries form.

The Common Chaffinch *Fringilla coelebs* (hereafter referred to simply as the 'Chaffinch') is notoriously variable across its Palearctic range. Cramp & Perrins (1994) divided the species into three distinct groups: the *coelebs* group of continental Eurasia, the *spodiogenys* group of Africa, and the *canariensis* group of the east Atlantic islands, which they suggested might be better regarded as three separate species. When one looks at the plumages of the males, these are indeed three distinct versions of Chaffinch, and many birders who have been to Gran Canaria or Tenerife to see the Blue Chaffinch *F. teydea* must have wondered whether there are, in fact, one or two more species of chaffinch to be ticked off.

The *coelebs* group of some ten races includes *gengleri*, found in Britain & Ireland, and *balearica* of Iberia and the Balearic Islands, while the *spodiogenys* group contains just the two races *africana* (Morocco to northwest Tunisia) and *spodiogenys* (rest of Tunisia and northwest Libya). The *canariensis* group comprises three races on the Canary Islands, namely *canariensis* of

Tenerife, Gran Canaria and Gomera, *palmae* of La Palma and *ombriosa* of El Hierro, along with *maderensis* of Madeira and *moreletti* of the Azores. The distributions of the races are shown in fig. 1.

Evolution and variation of the Atlantic-island Chaffinches have been studied previ-

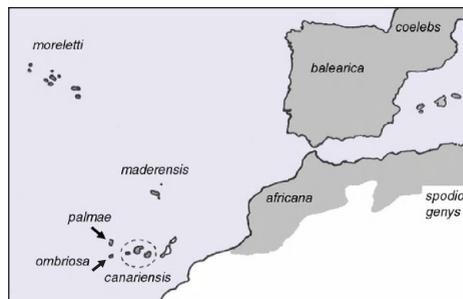


Fig. 1. Ranges of the races of Common Chaffinch *Fringilla coelebs*, adapted from Cramp & Perrins (1994).

Iberian birds are usually given the subspecific name *balearica*, differing from *coelebs* in measurements. This subspecies and the El Hierro form *ombriosa* were not recognised by Marshall & Baker (1999). The *spodiogenys* sample was collected at Nezfza, Tunisia.

ously on the basis of their morphology and behaviour (Grant 1979, 1980; Lynch & Baker 1993), and island populations are thought to have colonised from continental Africa or Europe in the last one million years. Critical to an evaluation of their taxonomic status is an assessment of the number of times the Atlantic islands were colonised from the mainland of Europe or Africa. For example, it would be predicted on the basis of geographical proximity that the Canary Islands are likely to have been colonised from Africa, whereas the Azores Chaffinches are more likely to have originated in Iberia. An alternative possibility is that birds from Africa or Europe originally colonised one of the Atlantic islands, and that this population subsequently expanded to the other islands. The latter scenario would imply that the plumage similarities among the Atlantic forms are due to their close relationships and common ancestor. Otherwise, if there have been two or more separate colonisation events, then we are forced to explain the morphological similarities of the different populations (large body mass, blue dorsal pigmentation, reddish-orange chest, short wings, long tarsi and long bill: Grant 1979) as being the result of convergent evolution in response to the peculiar environmental conditions common to the Atlantic islands. The two possibilities have very different implications for the taxonomic ranking of these forms, but morphological and distributional data alone cannot distinguish which is the more likely.

Genetic data, however, provide a potential means of shedding some light on their evolution. In a recent study, Marshall & Baker (1999) analysed four sequences of mitochondrial DNA (mtDNA) from various races of Chaffinch in order to identify the most likely colonisation history. They reasoned that, if the island forms of the Chaffinch originated as the result of a single colonisation event, followed by radiation to other islands, then it should be possible genealogically to trace all these forms to a single ancestor, so that they form a group which excludes the conti-

ental populations. If, on the other hand, there were two or more separate colonisations, we might expect DNA-sequence data to suggest, for example, that *canariensis* is more closely related to *africana* than to *moreletti* from the Azores; and also that it would not be possible to construct, on the basis of DNA, a genealogical tree which groups all the island Chaffinches together to the exclusion of mainland birds.

When Marshall & Baker collected DNA samples from Chaffinches, they found that there was little variation *within* most of the races, so the DNA sequences of representative individuals were fed into the analysis of variation *among* races. However, two different sequences of mtDNA were found in different individuals of both *canariensis* and *maderensis*, so these data were also incorporated (see figs. 2 & 3). Several different methods of resolving the relationships between the races were used (neighbour-joining, maximum-likelihood and parsimony-based analyses), producing five evolutionary trees. Four of the five analyses supported the hypothesis that a single colonisation event had occurred, such as the neighbour-joining tree presented in fig. 2.

A constant result, revealed in all five trees, was that *africana* is closely related to nominate *coelebs*; the two are sister taxa, more closely related to each other than they are to

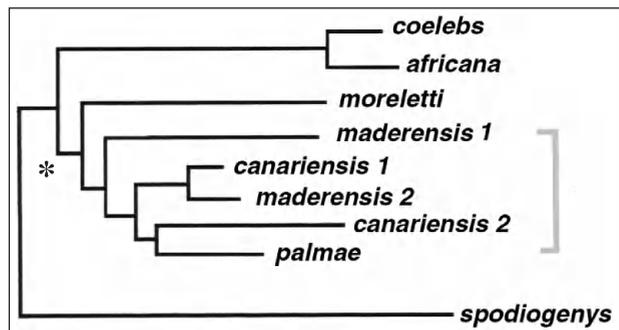


Fig. 2. Representative tree of the relationships between the various races of Common Chaffinch *Fringilla coelebs*.

The different mtDNA sequences found in different individuals of *canariensis* and *maderensis* are labelled arbitrarily '1' and '2'. Exact relationships among *canariensis*, *maderensis* and *palmae* are uncertain (indicated by grey bracket on right). It is possible to trace all the island birds back to a single ancestral, colonising, population (marked by an asterisk) which is separate from the lineage that led to *coelebs* and *africana*.

Redrawn from the neighbour-joining tree of Marshall & Baker (1999), and diagrammatic only; see Collinson (2001) for further explanation of the representation of phylogenetic trees.

any of the island forms, in spite of their very different plumage characteristics. Another constant result was that one of the *canariensis* mtDNAs (1 in fig. 2) clustered with one of the *maderensis* DNAs (2 in fig. 2), to the exclusion of the other *maderensis* and *canariensis* types. Marshall & Baker took this as evidence for some inter-island transfer of genes during the evolutionary history of Chaffinches. Different trees, however, differed in their interpretation of the relationships among the *maderensis*, *canariensis* and *palmae* individuals. What seems to have happened is that the original colonisation of one of the island groups was followed rapidly by radiation to the other islands, such that there was very little time for gene mutations to build up while the archipelagos were being actively colonised. The majority of the genetic differences among *canariensis*, *maderensis* and *palmae* have built up during the period since these forms were each isolated in their own separate ranges. The small number of shared mutations which might provide useful phylogenetic information are lost in the genetic 'noise' that has accumulated since isolation.

One tree (fig. 3), however, differed from the others in placing the divergence of the Azores birds, *moreletti*, near the base of the tree. Using this tree, it is no longer possible to trace all the island Chaffinches back to a single ancestor without also including the continental populations. It suggests early colonisation of the Azores by an ancestral chaffinch-type, followed by a later colonisation of the other islands by a common ancestor of the *coelebs/africana* birds. Although this tree is 'outvoted' 4:1 by the other trees, this does not necessarily mean that it is wrong; it could simply be the result of a more accurate methodology. Marshall & Baker used spectral analysis (a mathematical means of quantifying the amount of support and conflict for each proposed branching point in such a tree) to show that the 'multiple-

colonisation' result arose largely because of the weighting given to a mutation in a 'hotspot' (sequence of DNA where the mutation rate is higher than in surrounding sequences). It is very doubtful that this is a valid weighting, and the authors concluded that, although polyphyly (descent from more than one ancestral race) cannot be completely eliminated, it is much less likely than the alternative hypothesis, that all Atlantic-island Chaffinches arose from a single ancestral colonising population.

The genetic evidence is supported by studies of song patterns, measurements and protein polymorphisms. If we accept a rate of DNA divergence of 2% per million years per lineage as a rough calibration (Shields & Wilson 1987), then the ancestors of *moreletti* colonised the Azores approximately 600,000 years ago (presumably from Iberia), this being followed by rapid colonisation of Madeira and the Canary Islands. Although the phylogenetic trees could not resolve whether Madeira or the Canary Islands were colonised first, Madeira is geo-

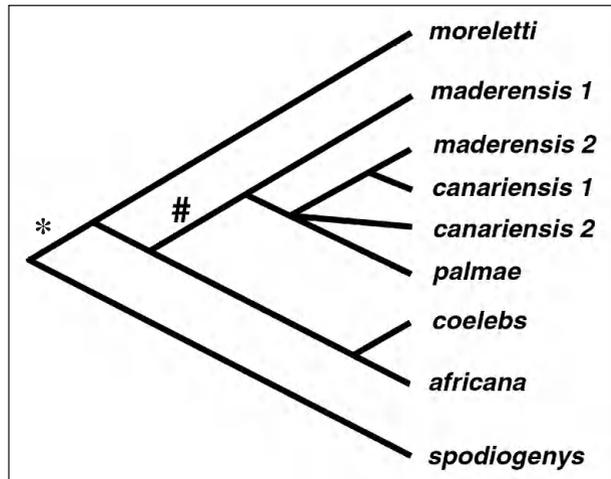


Fig. 3. A 'dissenting' tree which suggests at least two colonisation events by chaffinches *Fringilla*.

This tree, which fell out of a different analysis, has the Azores form (*moreletti*) separating from the ancestral lineage of chaffinches very early in its evolutionary history. In this case, the common ancestor of all island chaffinches (*) also gave rise to *coelebs* and *africana*. It suggests that, after chaffinches reached the Azores, a later-colonising lineage (indicated by #) which split off from continental chaffinches was the common ancestor of *palmae*, *canariensis* and *maderensis*.

Redrawn from Marshall & Baker (1999), who thought this tree to have been an artefact of the particular analysis technique (parsimony with transversion weighting), and therefore not likely faithfully to represent chaffinch evolution.

graphically the closer of the two to the Azores.

What does this mean with regard to Chaffinch systematics? As Marshall & Baker state, it is clear that the plumage similarities exhibited by the Chaffinches inhabiting the various east Atlantic islands are a result of these populations being descended from a common group of ancestors that colonised the Azores, and not the result of convergent evolution in response to similar island habitats. With the benefit of hindsight this is not surprising, since the Atlantic islands are in fact very different from one another in terms of, for example, climate and ecological pressures, and one would not expect any significant selection pressures operating on Chaffinches from different islands that would push these geographically separated populations into the evolving of a common morphology.

Summary and comment

European *coelebs* appears to be closely related to *africana*. This does not, of course, preclude the possibility that the two belong to different species. The big surprise, however, is that *africana*'s neighbour, the morphologically similar *spodiogenys*, is genetically divergent. A *spodiogenys* mtDNA sequence was found in a previous study to be intermediate between that of other Chaffinches and that of the Blue Chaffinch. If, as has been proposed, *africana* Chaffinches were to be split from *coelebs* because they are 'obviously different', then it is uncertain that *spodiogenys* could be uncritically included in the same species as *africana*, even though it is 'obviously similar'. This is a cautionary tale for the 'if it looks different, split it' band of birder-taxonomists.

It should also be noted that the study does not *prove* anything. For example, the evolution of these Chaffinches has taken place against a background of seven or eight glacial and interglacial periods, and there is any number of reasons why several colonisation and extinction events may have taken place which left no trace in the limited number of genes examined in this study. If there were ever short periods of extensive

gene flow among the different Chaffinch races, then we might get a false picture of the length of time which has elapsed since these races first diverged. On the basis of the available genetic evidence, however, the most likely scenario outlined by Marshall & Baker, which involves fewest assumptions and guesses, is as follows:

1. The *spodiogenys* haplotype, from Neza, Tunisia, is the remnant of an ancestral lineage linking Chaffinch with Blue Chaffinch.
2. About 600,000 BP, ancestral Chaffinches colonised the Azores, presumably from Iberia.
3. Shortly afterwards, a glacial period pushed all or part of these populations out of Iberia, with subsequent recolonisation from Africa during the interglacial (this would explain why *africana* and *coelebs* are so closely related).
4. Chaffinches quickly radiated out from the Azores, to Madeira and the Canary Islands, forming different subspecies as a result of founder effects, or natural selection, or both. On Gran Canaria and Tenerife, they would have met the Blue Chaffinch, the product of an earlier invasion (it has been suggested that the smaller, narrower bill of *canariensis* Chaffinches is a result of character displacement which avoids niche overlap with Blue Chaffinch).

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