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Colonization of Atlantic islands by chaffinches (*Fringilla* spp.)

by

P. R. GRANT, Ann Arbor

Studies of the evolution of birds on islands have contributed much to the development of ideas on speciation and other important areas of systematics (E. G. Mayr 1942, 1963, Rensch 1939). In attempting to interpret patterns of morphological variation on islands in terms of evolutionary processes, systematists are forced to make several assumptions. The purpose of this article is to make explicit three assumptions which are normally made implicitly, and to discuss them with an example from a recent study of chaffinches (Grant 1979a).

I compared the measurements of museum specimens of chaffinches *(Fringilla coelebs)* from two sets of Atlantic islands (Azores, and the Canaries including Madeira) and two sets of mainland regions (Iberia and North Africa). Two of the major results were as follows:

(1) On both sets of islands, chaffinches are heavier and have longer tarsi but shorter wings than their relatives on the mainland of approximately the same latitude.

(2) In mensural traits analyzed multivariately, Azores chaffinches are intermediate between chaffinches on the Canaries and the blue chaffinch, *Fringilla teydea* on two Canary Islands, Tenerife and Gran Canaría.

The first result was interpreted as showing convergent evolution of chaffinches in separate island environments. This interpretation is reinforced by the blue cast to the plumage of all the island chaffinches in contrast to all mainland chaffinches. The second result was interpreted as possible evidence of character displacement (Brown & Wilson 1956; Grant 1972a). It was suggested that the blue chaffinch, the first species to arrive on the Canaries, diverged in beak form and specialized in pine forest exploitation following the later arrival of the chaffinch. The intermediate morphological nature of the Azores chaffinch was held to indicate what the blue chaffinch was approximately like on the Canary Islands before the character displacement occured.

The interpretations are no stronger than the assumptions upon which the original analyses rest. These will now be considered.

Assumptions

The first assumption is that morphological differences between populations reflect genetic differences to some extent. It is known that the climatic conditions under which birds are reared can influence adult morphology (e.g. Allee & Lutherman, 1940), and that diet of seed-eating birds influences beak growth (Sossinka, 1972). Therefore direct environmental influences may differ between populations and contribute to differences in adult morphology. But they are not likely to be responsible for large and non-allometric changes in proportion (Grant, 1972b). Estimates of the amounts of direct environmental and genetic influence on adult morphology are badly needed to check on this, as they are for morphological studies of non-domestic birds in general. A few studies have demonstrated the presence of genetic variation underlying phenotypic variation within populations of birds (Boag & Grant 1978, Smith 1979). This evidence strengthens the argument that phenotypic differences between populations are partly determined by genetic differences, but experimental evidence is needed to convert the argument into a demonstrated fact.

The second assumption is that present mainland populations are morphologically close to the ancestral stocks which gave rise to the island populations. Therefore, the present differences between mainland and island populations are largely the product of evolutionary changes on the islands. The alternative is that mainland populations have evolved considerably since giving rise to the island populations, or that they have shifted geographically in response to climate, as a consequence of which populations on the mainland adjacent to the islands are not the appropriate ones for making comparisons with island populations. I regard these alternatives as less likely than the assumed morphological constancy on the mainland. There is much evidence for relatively rapid evolution in isolated populations (Cain, 1954, Mayr, 1963, Johnston & Selander 1964). In the case of Atlantic Island chaffinches, a geographical shift in mainland populations would result in inappropriate island-mainland comparisons. However geographical variation on the mainland is relatively small, and the comparisons would not be distorted strongly enough to alter the interpretations of the evolution of birds on these islands (see also next paragraph).

The third assumption merits the most discussion. It is that the archipelagos were colonized independently from the adjacent mainlands at approximately the same latitude, i.e., from the geographically closest points on the mainlands to the islands. This may not be correct. With very isolated islands, like the Azores, it is especially difficult to identify the point of origin of the colonists. However, in the case of the Azores an incorrect assumption about the place of origin of the colonists is not likely to lead to erroneous conclusions regarding the evolutionary change that has taken place on the islands.

This is because the most likely alternative to an Iberian origin is one further north where chaffinches are slightly smaller than in Iberia. An origin further north is indicated by present wind patterns. Winds rarely blow to the Azores directly from the east (i.e. Iberia); they arrive much more frequently from the north or the north-east (Bannerman & Bannerman, 1966).

The origin of Canary Island chaffinches is apparently more readily identifiable. The Canaries are much closer to North Africa than the Azores are to anywhere. There are faunistic similarities between the Canaries and North Africa (Lack & Southern, 1949) and the blue tit, the only other bird species showing similar differentiation in the archipelago to the chaffinch, is clearly related to the Moroccan blue tit (Grant 1979b). The assumption of a North African origin of Canary Island chaffinches may, nevertheless, be wrong. The major alternative is an Azores origins, (another is an Iberian origin), improbable as this may seem from distance considerations alone.

First, there are strong winds blowing southeastwards from the Azores to the Canaries in winter (Fernandopullé, 1976) when chaffinches are in flocks of substantial size and are perhaps most likely to disperse. Second, there is a close resemblance between Azores and Canary Island chaffinches in those plumage characteristics which set all island populations apart from all mainland ones. The dorsal plumage is largely a slateblue colour, and the ventral plumage is buff and white. In such characeristics, they show a loss of red and green colour; reds are virtually absent and green is restricted to back, rump and the edges of wing feathers. Third, there is a progressive loss of green from Azores (the most green), to Madeira (almost the same) to the central Canary Islands (no green on the back) to the western ones (no green at all). Fourth, some mensural characteristics of Azores and Canary Island populations are related to each other in the same way as they are related in South European and North African populations (Grant 1979a). For example, weights are apparently the same on the Azores and Canaries, and apparently the same in France and North Africa, but differ greatly between regions. Moroccan birds have slightly longer wings (by 3.38 per cent) and tarsi (by 2.74 per cent) than Iberian birds, and Canary birds differ from Azores birds in the same direction and by approximately the same amount (1.40 and 2.31 per cent respectively). These similarities could be the result of the derivation of one set of island populations (Canaries) from the other set (Azores), just as the North African populations are probably derived from European ones.

As indirect support for an Azores origin, there is one other species of bird which appears to have colonized the Canaries from somewhere in Europe, possibly the Azores. This is the robin, *Erithaca rubecula*. Robins on Gomera, Hierro, La Palma and Madeira are a slightly paler version of the South European robin, *E. r. rubecula,* but are sufficiently different to be considered by

some taxonomists as a distinct subspecies, *E. r. microrhynchus* (Bannerman, 1963). They have similar altitudinal distributions and occupy similar habitats. It is possible that these Canary robins originated from the Azores and not from mainland Europe because Azores robins share the pale colour. A North African origin of these populations can be ruled out for the interesting reason that Tenerife and Gran Canaría have been colonized by the distinctive North African subspecies. Like the Moroccan relatives, robins on these two islands have dark pigments and are restricted to mountain forests (Bannerman, 1963). Therefore, the Canary Islands have been colonized by robins from both North Africa and Europe, possibly the Azores.

For these several reasons an Azores origin of the Canary Island chaffinches is a serious alternative to the assumed North African origin. What are the possible consequences of this alternative? First, if this alternative is correct, features in common to Azores and Canary populations are not the product of convergent evolution to common environmental conditions, but are carry-overs from evolution on the Azores. These features include blue pigmentation in response to high humidities, short wings and long tarsi. Note however, that whatever the origin of Canary Island chaffinches, beak shape has undergone substantial change there; beaks are smaller, particulary in depth, than on the Azores or on the mainland.

A second consequence is more important, but also more problematical. If Canary Islands birds are derived from Azores populations, the question of character displacement between the chaffinch and the blue chaffinch has to be reconsidered.

The blue chaffinch is generally agreed to be the evolutionary product of an early colonization of the Canaries by the ancestors of the modern chaffinch (Stresemann 1927-1934). Whether the Canary Island populations of the blue chaffinch are the sole surviving members (relicts) of a once widely distributed species, or whether the species evolved into its present form entirely on these two islands (Tenerife and Gran Canaría), cannot be known in the absence of fossils. A second, much later colonization gave rise to the present-day populations of the chaffinch on the Canaries. By analogy with the robin, discussed above, the geographical sources of the two sets of colonists may have been quite different. For example the first colonists which gave rise to the blue chaffinch may have originated in North Africa, and the second colonists may have come from the Azores; alternatively both sets of colonists may have come from the Azores.

Regardless of the point of origin of the blue chaffinch, what evidence of character displacement is provided by the chaffinch? The unusual shape of the beak on all the Canary islands can be interpreted as a divergence from the blue chaffinch on Tenerife and Gran Canaría, with no relaxed or different selection pressure on the other islands without the blue chaffinch. This

explanation is consistent with a colonization of the islands by chaffinches from North Africa, since Tenerife and Gran Canaría where the initial adaptations occurred, are the easternmost Canary Islands supporting populations of chaffinches. But it is not consistent with an Azores origin of the chaffinch. Beak shape and size is almost identical on Madeira and Gran Canaría, yet presumably Madeira (without the blue chaffinch) would have been the first island colonized and hence the place where the Canary Island characteristics of the chaffinch would have first evolved. The only way to rescue the character displacement hypothesis for the chaffinch is to make the additional, and perhaps improbable, assumption that the blue chaffinch occurred on Madeira when the chaffinch arrived, but since went extinct. A reason for extinction is not easy to find; competitive exclusion by the chaffinch is certainly not likely, because the island elevation and extent of pine forest is greater on Madeira that on Tenerife and Gran Canaría.

In sum, the blue chaffinch may have undergone character displacement following the arrival of the chaffinch on the Canaries. Whether or not the chaffinch can be considered to have undergone character displacement as well is dependent upon the source of the second colonists, the Azores or North Africa.

Discussion

There are obviously limits to the success we can achieve in resolving these problems concerning the origin and subsequent evolution of Atlantic Island chaffinches. The same may be said about birds in other archipelagos, such as the Hawaiian Drepaniidae (Amadon 1950, Bock 1970) and Darwin's Finches (Geospizinae) on the Galápagos and Cocos Island (Bowman 1961, Grant 1967, Lack 1947). I suggest that refinement of modern biochemical techniques holds the best hope for establishing affinities between populations of the same species. At the moment such techniques as electrophoresis, microcomplement fixation and DNA-DNA hybridization are most succesful at genus and higher taxonomic levels (Barrowclough & Corbin 1978, Ford et al. 1974, Polans 1980, Prager & Wilson 1975). Interpretation of the evolution of island populations will be on a firmer foundation once colonization routes have been determined with greater certainty.

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Address of the author: Prof. Dr. P. R. Grant, Division of Biological Sciences, Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan 48109, U.S.A.