BIOMETRICS AND ORIGINS OF SOME ATLANTIC ISLAND BIRDS

By M.V.HOUNSOME[1]

ABSTRACT. The biometrics of living birds captured for ringing in Madeira and Britain indicate that:
1) The wings of Atlantic Island Blackcaps, Chaffinches, Robins and Blackbirds are shorter than those of the continental forms, but only those of Blackcaps and Chaffinches are rounder. 2) Other dimensions of several species show differences, but they are not consistent between species. 3) Not enough data were available to test the extent of sexual dimorphism, although Madeiran Firecrests are not sexable on crest colour. 4) Madeiran Canaries have shorter wings than Canary Island Canaries, and are similar in this respect to Serins. 5) Some of these findings are characteristic of the 'Island Syndrome'.

Discriminant Function Analyses based on 214 museum skins from the Azores, Madeira, the Canaries, Europe and North Africa indicate that:
1) The three endemic pigeons of Madeira and the Canary Isles are distinct species, the two Canarian species being most closely similar. 2) Madeiran and the western Canary Robins are indistinguishable but are distinct from the nominate; thus *Erithacus rubecula microrhyncus* Reichenov 1906 should be accepted as a valid subspecies. 3) Madeiran Blackcaps and Blackbirds are closest to European ones, and Canarian Blackcaps and Blackbirds are closest to North African ones. 4) *Turdus merula agnetae* Volsøe 1949 is a good subspecies. 5) Madeiran and Canarian Firecrests are both distinct from the nominate subspecies, with the Balearic birds being less so. 6) Madeiran Rock Sparrows are barely distinguishable from the nominate, but are distinct from the North African birds. 7) Madeiran and the various subspecies of Canarian Chaffinches are all distinct, but are more similar to each other than they are to European or North African birds.

To draw evolutionary conclusions from these findings one must accept that overall similarity reflects ancestry - a traditional, non-cladistic view not currently popular.

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INTRODUCTION

One of the perennial topics of island zoogeography has been the colonisation, evolution and extinction of island forms; and one of the prerequisites of such studies is an assessment of the nature and extent of the physical and genetic differences between island forms and their continental cousins. In the nineteenth and early twentieth centuries most interest was directed towards the description of new 'species'. The species concept has undergone (and is undergoing) several changes since then - many 'species' being relegated to 'subspecies or simply 'forms' or 'populations'. What remains true is that island animals are often identifiably different from their continental neighbours, whatever taxonomic level is used to describe them. Moreover, it has been asserted that there are certain trends in these differences that occur time and again, and which collectively have been described as the **Island Syndrome** (Blondel, 1985).

The Island Syndrome includes some of the following characteristics:

1) Shorter, more rounded wings
2) Longer bills and tarsi
3) Increased biometric variability
4) Duller, less distinctive plumage
5) Less sexual dimorphism
6) Smaller size, except for carnivores and flightless species, which may be larger
7) Wider niche occupation, at least in the early stages of colonisation
8) Fewer species per unit area
9) Higher population densities
10) Lower fecundity, with higher adult survival

None of these is invariably present, and there are many exceptions, but most island avifaunas exhibit most of these characteristics. The first is found in more sedentary populations and eventually results in flightlessness. The second enables the exploitation of a wider range of foods and habitats. The third may be due to 'character release' in the absence of competitors. The fourth and fifth are widely held to be true (Lack, 1947; Moreau, 1966), but need to be investigated; if true, then they have consequences for models of sexual selection as well as speciation (Baker & Hounsome, 1983). The situation as to the sixth is confused, and needs to be clarified. Consideration of the last four characteristics is outside the scope of this paper, but it is impossible for ornithologists visiting Madeira, for example, not to notice that the Firecrest (*Regulus ignicapillus madeirensis* Harcourt, 1851) is found in circumstances reminiscent of *Phylloscopus* warblers and even Wrens (*Troglodytes troglodytes troglodytes* (L)) in continental Europe. Nor can one fail to notice the wide variety of calls uttered by Madeiran birds compared with their continental forms. The various stages in niche occupation and speciation have been described as a 'Taxon Cycle', which has been investigated on Madeira by Jones *et al* (1987).

Once differences in populations have been identified it then becomes possible to ask how they came about, and what relationship do the populations bear to each other. One possible approach to these questions involves measuring *how* different the populations are - the extent of the differences being likely to be proportional to how closely related they are. This way of thinking is firmly in the established, morphological, taxonomic tradition rather than the cladistic one. The first part of this paper reveals some biometric differences relevant to the Island Syndrome, and the second explores how far one can go in drawing evolutionary conclusions from biometric data.

BIOMETRICS

Wing Length and Shape

Wing length is easy to measure, but there are difficulties in comparing measurements taken by different investigators, and when comparing measurements of live birds with those of museum skins. In this paper most of the measurements were taken by one team (whose measurements agree) on either live birds or skins, but not both together. Exceptions to this are noted in the text.

Wing shape can be defined by the relative or absolute lengths of the primary feathers (figure 1). Pointed wings have long outer primaries, and round wings have short ones; the outermost primary is usually small or almost absent in European passerines. While this method of describing wing shape is effective, it is time-consuming and does not lend itself to simple analysis. Many indices of roundness have been proposed, but one of the simplest and most effective has been that of Gaston (1974), where the length of the innermost primary is expressed as a fraction (or a percentage) of the maximum cord wing length. The length of the innermost primary is a measurement of the width of the wing, so it is easy to see that Gaston's index is a measure of the wing's width to length ratio. In practice one measures the wing length (L) and the difference, on the folded wing, between the tip of the wing and the tip of the innermost primary (x). The index of roundness is (L-x)/L. Gaston (1974) does not give a test for the significance of the difference between indices.

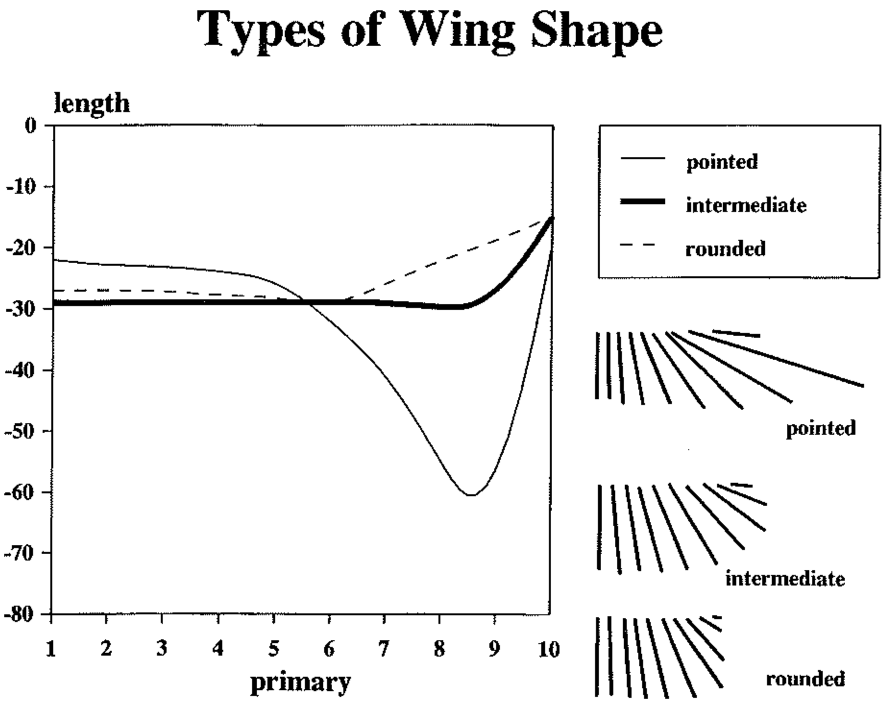

Figure 1. Three type of wing shape; primaries numbered descendantly; lengths of each feather, in millimetres, on a negative scale to reflect the wing as seen on the bird in the hand.

The wing shapes of three populations of Blackcap (*Sylvia atricapilla*) are shown in figure 2; the measurements are all of live birds. The inclusion of resident Gibraltan birds illustrates the fact that 'island forms' can occur on peninsulas. This Gibraltan 'form' was noted by Finlayson (1981) but has yet to be formerly described. It is resident on Gibraltar and is joined in the migration seasons by passage birds going to and from the rest of Europe. Figure 2 shows that Madeiran Blackcaps (*Sylvia atricapilla heineken* Jardine 1830) and the Gibraltan form both have shorter wings than British Blackcaps (*S.a.atricapilla* (L)). Gaston's indices (table 1) show little difference between Gibraltan and Madeiran Blackcaps (80.9 and 79.2 respectively), both of them having more rounded wings than the nominate subspecies (78.1 from Britain, and 77.9 for *passage* birds from Gibraltar), and thus exhibit part of the Island Syndrome.

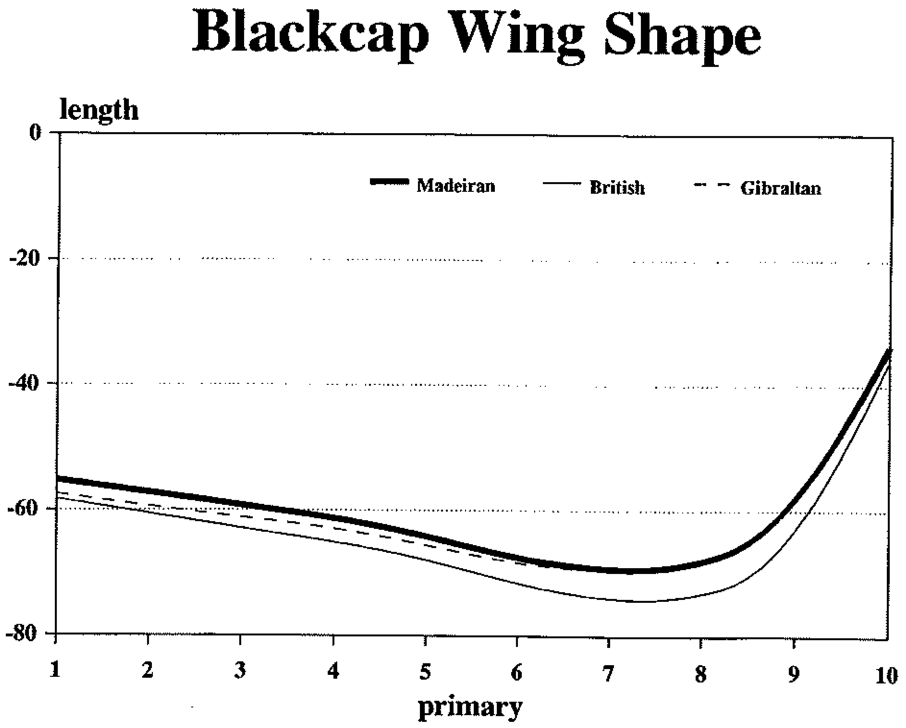

Figure 2. Wing shape of three populations of Blackcap (*Sylvia atricapilla*); conventions as in Fig.1

BLACKCAP	Gibraltan "form"	Madeiran *S.a.heineken*	British (nominate)	Nominate on passage (Gibraltar)
Wing Length	68.6 ± 2.19	69.7 ± 1.60	74.5 ± 1.79	74.1 ± 1.87
Roundness	80.9	79.2	78.1	77.9

Table 1. Wing length (mm ± sd) and index of roundness of four populations of Blackcap, sexes combined. Gibraltan data from Finlayson (1981), Madeiran and British data from the author's ringing records.

Madeiran Chaffinches (*Fringilla coelebs maderensis* Sharpe, 1888) have shorter, more rounded wings than nominate British ones (table 2). This roundness is achieved by the outermost four primaries being shorter, while the inner four or five are longer (figure 3). This is not a simple shortening of the wing and could be taken to indicate a considerable degree of progress along the Taxon Cycle route, implying a long period of isolation from continental populations.

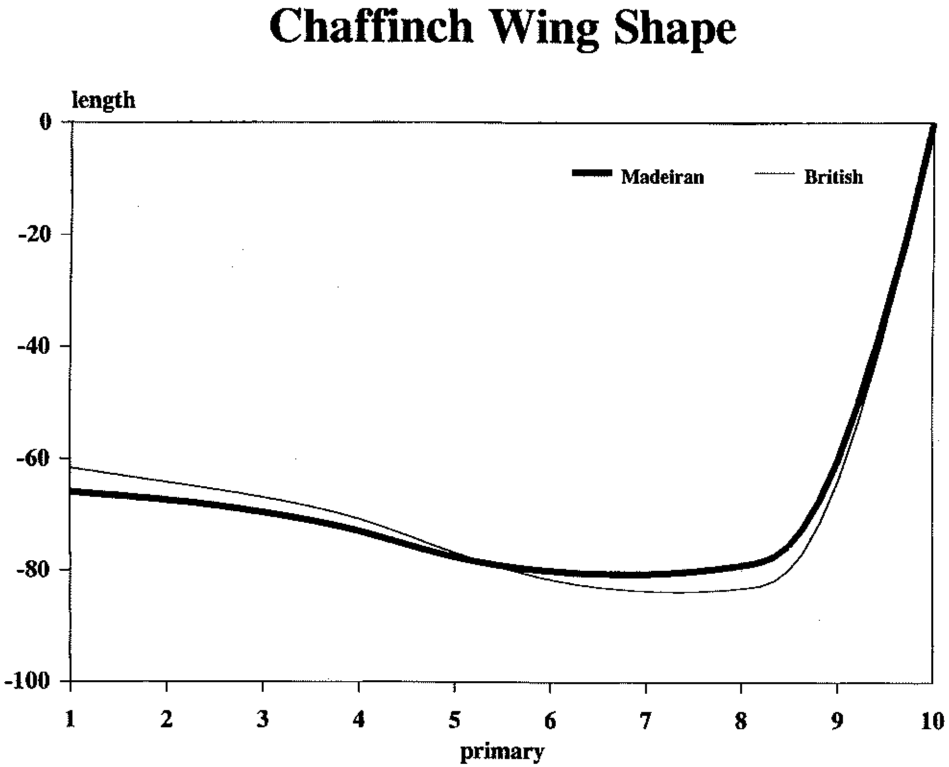

Figure 3. Wing shape of two populations of Chaffinch (*Fringilla coelebs*); conventions as in figure 1. The outermost, 10th, primary is minute in both populations.

		British	Madeiran
CHAFFINCH	Wing Length	83.95 ± 3.31	81.23 ± 3.40
	Roundness	73.3	81.2
ROBIN	Wing Length	73.52 ± 2.01	70.50 ± 2.19
	Roundness	83.0	81.6

Table 2. Wing length (mm ± sd) and index of roundness of British and Madeiran Chaffinches and Robins, sexes combined. Data from author's ringing records.

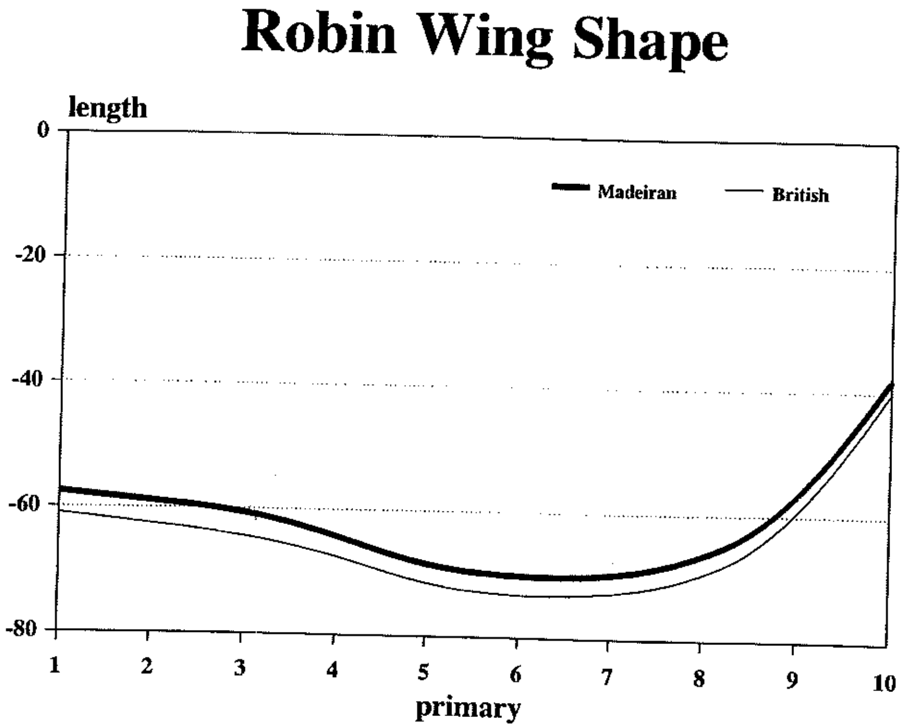

Figure 4. Wing shape of Madeiran and British Robins (*Erithacus rubecula*); conventions as in Fig.1.

The Madeiran Robins (*Erithacus rubecula* (L)), on the other hand, have shorter wings than British ones (figure 4), but they appear to be *less* rounded (81.6 as opposed to 83.0, table 2). Some authors, notably Bannerman & Bannerman (1965), have regarded the Madeiran Robin as subspecifically distinct from the nominate, identifying it as *E.r.microrhyncus* Reichenow 1906, the subspecies also found on La Palma, La Gomera and Hierro in the Canaries. Modern practice is to regard the Madeiran Robins as belonging to the nominate subspecies. The evidence of figure 4 indicates that they are not the same as the nominate subspecies, but does not help in deciding whether they are different enough to be put into another subspecies, nor, if so, whether it should be *E.r.microrhyncus*. Further evidence on this subject will be presented in the Discriminant Function Analysis section of this paper.

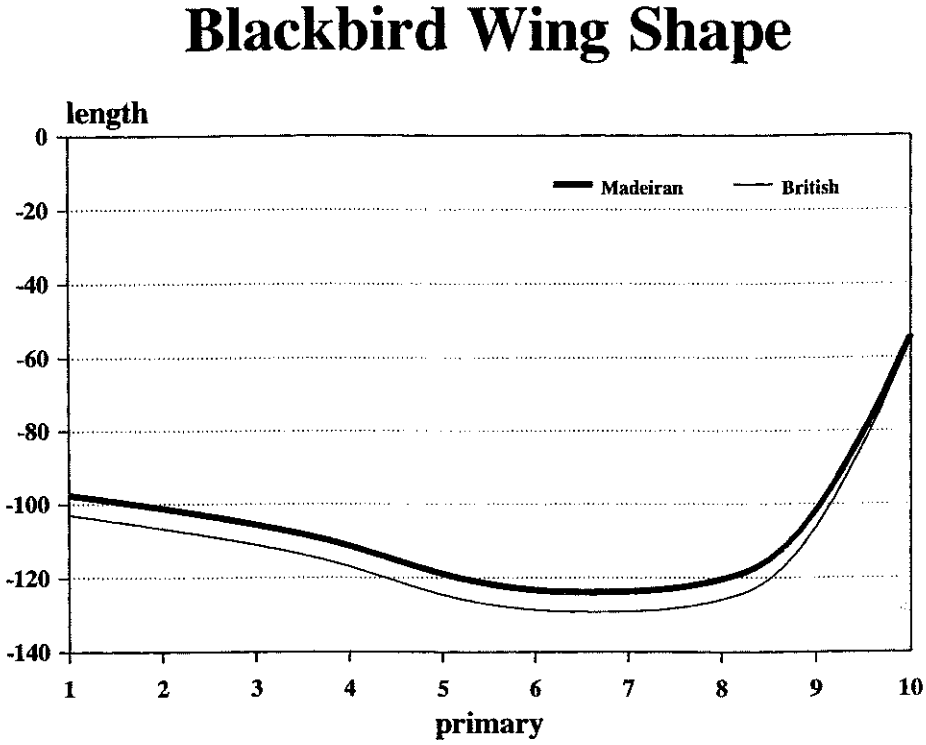

Figure 5. Wing shape of Madeiran and British Blackbirds (*Turdus merula*); conventions as in Fig.1.

Gaston's index is the same for British and Madeiran Blackbirds, but the Madeiran birds (*Turdus merula cabrerae* Hartert, 1902) have shorter wings than the nominate subspecies (figure 5).

Other Biometric Data

A rough summary of the differences in measurements between some common passerine species is shown in table 3. A full statistical analysis would be necessary to establish the significances of these apparent differences, but the purpose of this paper is to point out likely areas of interest in the subject of the biometrics of North Atlantic Island birds, not to present a completed analysis. While most of the measurements in table 3 indicate that Madeiran birds are smaller than British ones of the same species, this is not uniformly so. It seems likely that Madeiran Chaffinches have longer bills and tarsi, and that all the species weigh less, thus exhibiting the Island Syndrome. Madeiran Robins (*Erithacus rubecula microrhyncus* Reichenow 1906) and Linnets (*Carduelis canabina nana* (Tschusi, 1901)) are smaller in all dimensions, except that the latter have longer tails, like Twite (*C.flavirostris* (L)).

The hypothesis that sexual dimorphism is less distinct on islands is not supported by the mean female measurements as a percentage of mean male ones, table 4. The numbers of Madeiran birds measured is small, so little reliance can be placed on the precise figures, but there is no discernible trend, however insignificant, in this table. More live measurements of Madeiran birds are required to establish whether there are real differences.

SPECIES	WING	BILL	TARSUS	TAIL	WEIGHT
Blackbird	-5	+1	0	-3	-7
Blackcap	-4	+0.5	0	0	m=0, f-2
Chaffinch	-3	+2	+3	-5	m+2, f=0
Goldfinch	-3	-1	-1	-2	-2
Grey Wagtail	m=0, f+2	+0.6	0	m-9, f-3	m-3, f-1
Linnet	-7	-1.5	-1	+2	-6
Robin	-3	-1.5	-1.5	-1	-3

Table 3. Approximate differences (mm and gms) between Madeiran and British birds (Madeiran - British).

SPECIES	SUBSP.	WING	BILL	TARSUS	TAIL	WEIGHT
Blackbird	British	96.59% n=375	98.36% n=323	99.04% n=323	96.32% n=323	102.60% n=377
	Madeiran	97.61% n=12	99.05% n=12	98.97% n=12	96.57% n=12	106.99% n=12
Blackcap	British	100.4% n=213	99.79% n=170	102.0% n=170	100.5% n=170	103.94% n=214
	Madeiran	97.58% n=19	103.5% n=19	100.4% n=19	96.93% n=19	113.64% n=18
Chaffinch	British	94.58% n=122	97.55% n=108	100.2% n=108	93.14% n=108	93.49% n=122
	Madeiran	94.36% n=11	96.97% n=11	94.68% n=11	94.25% n=11	84.27% n=11

Table 4. Mean Female measurements as a percentage of mean male measurements. Data from author's ringing records.

The difficulties in comparing measurements taken in different places, or at different times, by different people are illustrated in table 5. Bulwer's Petrels (*Bulweria bulwerii* Jardine & Selby, 1828) has a worldwide oceanic distribution, and one might expect large differences between the biometrics of the various populations. On the other hand, if there is movement between colonies, one might expect little difference. Certainly there is no compelling evidence in table 5 of a difference between the samples. Statistical analysis would not help here, because of the differences in the collection of the data noted above, and because some measurements were taken from live birds and some from skins.

A biometrical curiosity that should be reported concerns the Madeiran Canaries (*Serinus canarius* (L)). Table 6 shows some biometrics of Madeiran and Canary Island Canaries and European specimens of Serin (*S.serinus* (L)). In all but one respect the Madeiran and the Canary Isle Canaries are indistinguishable and are different from European Serins (t-tests between the two populations of Canaries all with $p<0.04$, and between both populations of Canaries and the Serins all $p>0.4$). The exception is the wing length, in which the Madeiran Canaries are different from the Canary Isle Canaries ($t=2.60$, $p=0.021$) and indistinguishable from Serins ($t=0.26$, $p=0.794$). The difference cannot be due to skin shrinkage, as the smaller mean is from the live specimens, not from preserved skins. Does this indicate a first step towards the evolution of a distinctly Madeiran population?

	WING	BILL	TARSUS	TAIL	WEIGHT
World	197.5, n=40 187-219	21.5, n=40 19.5-23.3	26.7, n=40 24.2-29.0	-	94.8, n=40 71-117
Desertas	198.2, n=5 196-201	21.1, n=5 20.5-21.8	26.2, n=5 25.8-26.8	-	93.4, n=5 87-98
Deserta Grande	202.8, n=123 195-211	21.5, n=123 19.5-23.5	27.7, n=123 21.5-30.0	109.0, n=123 103-118	86.7, n=123 69-114
Canaries	204.8, n=12 201-210	22.5, n=12 21.1-23.4	26.6, n=12 25.6-28.2	111.9, n=12 107-114	-
Hawaii	199.0, n=14 190-202	21.9, n=14 21.0-22.8	26.1, n=14 24.0-27.8	113.0, n=14 107-117	-

Table 5. Dimensions of Bulwer's Petrels (mm, n, and range): World and Desertas - skins in Paris museum (Jouanin *et al*, 1979); Deserta Grande - birds trapped and ringed by Manchester University expedition, September 1981; Canaries and Hawaii from Loomis 1918. Sexes combined.

	WING	BILL	TARSUS	TAIL
Canary Island Canaries	73.8 ± 1.60 n=6	10.5 ± 0.63 n=6	17.2 ± 0.68 n=6	56.3 ± 1.94 n=6
European Serins	71.8 ± 1.90 n=13	9.5 ± 0.54 n=13	15.7 ± 0.75 n=13	48.0 ± 2.30 n=13
Madeiran Canaries	71.6 ± 1.66 n=10	10.2 ± 0.82 n=10	17.1 ± 0.90 n=10	57.0 ± 1.26 n=10

Table 6. Dimensions of Canaries on Madeira and the Canary Isles *Serinus canarius* and of European Serins *Serinus serinus* (mm ± sd). Data from skins in the Manchester Museum (Canary Island Canaries and European Serins) and from live Canaries trapped on Madeira.

This first section has pointed out that, even for a group as well studied as the birds, on islands as accessible as Madeira and the Canaries, we still do not have enough biometric data to answer all the questions that need to be answered before we can describe the nature of the island populations and their evolution. A full analysis would require integration of the biometric data with the fossil evidence. Nevertheless, simple measurements of the existing bird populations can still reveal many interesting relationships.

DISCRIMINANT FUNCTION ANALYSIS

There are many ways of analysing the physical differences between groups of organisms, but Discriminant Function Analysis (DFA) is one of the most powerful and visually informative. DFA has been in use for many years, but it is only since the advent of computers that it has been easily available. The SPSS computer package, first on mainframes then on personal computers, has done much to make DFA universally accessible. In essence, DFA provides a set of functions, or equations, in which the differences between declared groups are maximised. The number of possible functions is one less than the number of groups entered into the analysis. It may be that just one function is enough to distinguish the groups, but usually two or more are necessary. It is easy to plot the function values for one or two functions, or even three (if one can produce and interpret three-dimensional graphs), but n-dimensional analyses are impossible to envisage, although they may have biological meaning.

Museum bird skins from the Azores, Madeira, the Canaries, North Africa and Europe were studied at Manchester University Museum, Merseyside County Museum (now The National Museums on Merseyside), and the British Museum (Natural History) (now The Natural History Museum). Standard museum measurements were made (wing, bill, tarsus, tail), together with bill depth and primary feather lengths and emarginations. Each specimen was also scored for up to seven plumage characters that were devised for each species, usually on a scale of 1 to 3. The results for the males of seven species, or species groups, are presented here. Each species heading is followed by the percentage of specimens correctly assigned to its group by the DFA, and the extra characters used for that species.

Pigeons (100%; middle toe length, back colour, neck iridescence, belly colour, tail tip colour, crown iridescence, bill width). Figure 6.

Three closely related endemic pigeons occur, or used to occur, on Madeira and the Canaries: the Trocaz or Long-toed Pigeon (*Columba trocaz* Heineken, 1829) on Madeira; Bolle's Pigeon (*C.bollei* Godman 1872) on

Tenerife, La Palma, La Gomera, and Gran Canaria; and the Laurel Pigeon (*C.junoniae* Hartert 1916) on La Palma, La Gomera and Tenerife. Vaurie (1965) regards *C.bollei* as a subspecies of *C.trocaz*, but most modern authors (Cramp *et al*, 1985) regard them as separate species.

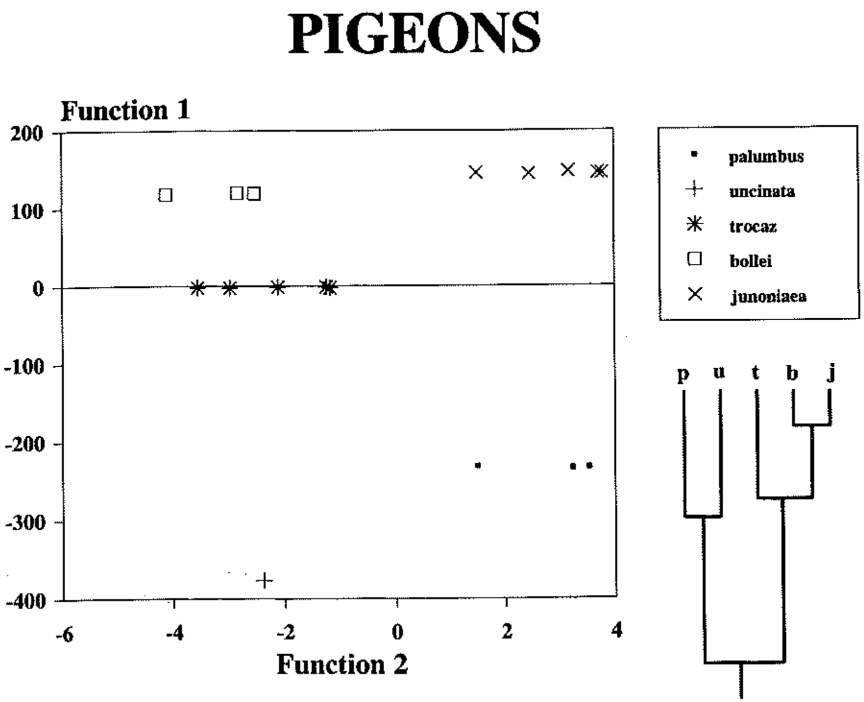

Figure 6. Plot of the first two functions discriminating between the three Atlantic Island Pigeons (*Columba* spp), the European Wood Pigeon (*C.palumbus*), and an African 'out-species'(*C.uncinata*).

For the discriminant analysis of these taxa three specimens of Woodpigeon (*C.palumbus* L) and one of Afep Pigeon (*C.uncinata* Cassin 1860, an African species) were included as 'outgroups'. Plots of the first two functions are shown in figure 6. It can be seen that the Woodpigeon and the Afep Pigeon are indeed 'outgroups', but that *C.bollei* is closer to *C.junoniae* than to *C.trocaz*.

The dendrogram (figure 6) was constructed using the Euclidian distances between the group centroids, and can be interpreted as representing the degree of physical similarity between the groups. On the basis of this evidence, therefore, it seems that the three species of endemics are indeed separate. Furthermore, it suggests that the Canary Island species are more similar to each other than they are to the Madeiran species. Zoogeographically, this is not surprising.

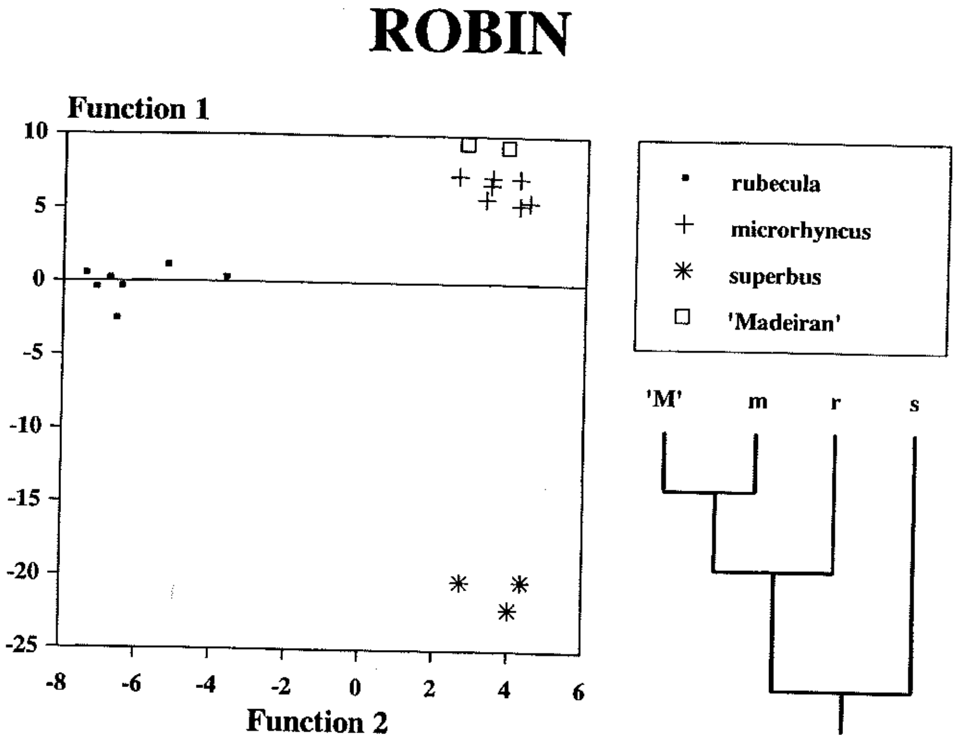

Figure 7. The first two functions discriminating between four populations of Robin (*Erithacus rubecula*).

Robin (100%; intensity of breast colour, belly buffness, under-tail covert rufousness, back darkness). Figure 7.

It is generally accepted that there are two subspecies of Robin on the Canaries: *Erithacus rubecula superbus* Koenig 1889, which is confined to Gran Canaria and Tenerife, and the nominate, which occurs on the western Canary Islands and which is also found on Madeira. The non-*superbus* Robins of the Canaries and Madeira have also been described as *E.r.microrhyncus* Reichenow 1906, but this subspecies is not widely accepted.

In the DFA the Madeiran Robins were entered as a separate group because of the possibility of their being distinct. In fact, the DFA supports Reichenow's results, in that the western Canary Robins are indistinguishable from the Madeiran ones, but that they are both distinct from the nominate; *E.r.superbus*, as expected, is quite distinct from all the other groups. If this analysis is valid, then Reichenow's subspecies should be reinstated.

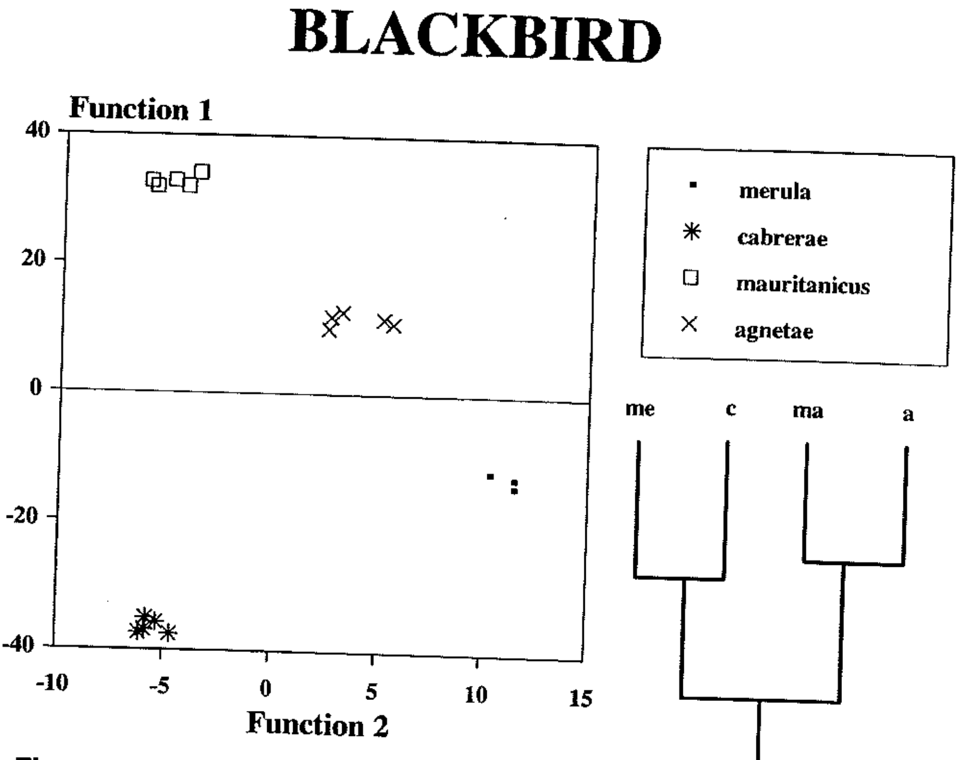

Figure 8. The first two functions discriminating between four sub-species of Blackbird (*Turdus merula*)

Blackbird (100%; blackness of plumage). Figure 8.

Most modern authors (Cramp 1988, Vaurie 1959) consider that the Blackbirds of Madeira and the Canaries are both referable to *Turdus merula cabrerae* Hartert 1901, in spite of the Canary form being described as *T.m agnetae* by Volsøe in 1949. The DFA (figure 8) supports Volsøe's subspecies, as *T.m.agnetae* is closer to the North African *T.m.mauritanicus* Hartert 1902 than it is to either the nominate or the Madeiran subspecies. If this analysis has any validity, then it is likely that the Canaries were colonised by Blackbirds from North Africa, whereas Madeira was colonised from continental Europe. There were no skins of the Azorian Blackbird (*T.m.azorensis* Hartert 1905) available for analysis.

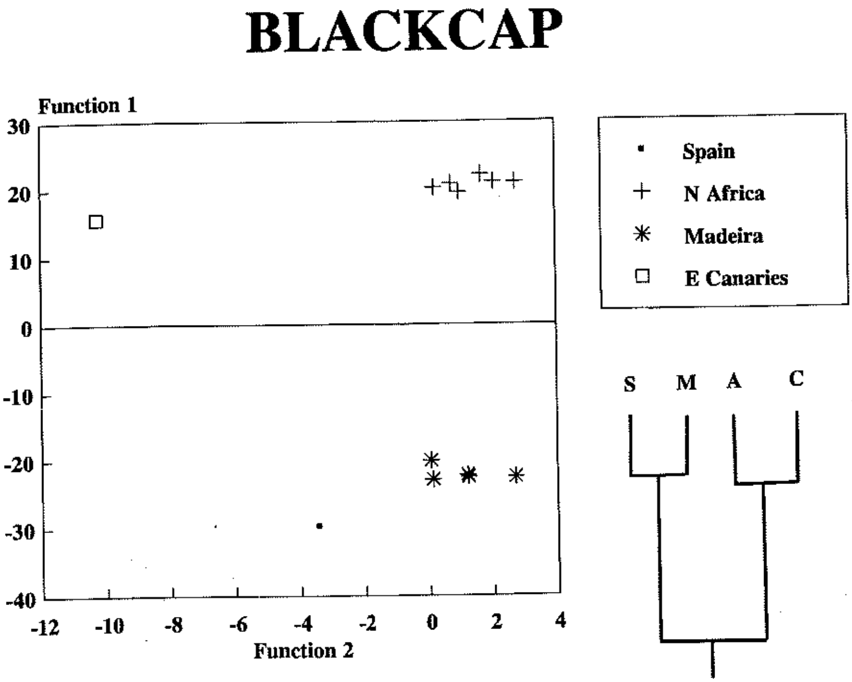

Figure 9. The first two functions discriminating between Blackcaps (*Sylvia atricapilla*) from four regions.

Blackcap (100%; darkness of back). Figure 9.

There are only three recognised subspecies of Blackcap (*Sylvia atricapilla* (L)) in the western palaearctic: the nominate, a summer visitor found over most of the area, *S.a.pauluccii* Arrigon1 1902, which is confined to Sardinia and the Balearic Islands, and *S.a.heineken* (Jardine 1830), which occurs only on Madeira.

For the DFA it was decided to group the specimens not by subspecies but by geographical area, as there were only two subspecies to be considered (*S.a.pauluccii* being out of the area of interest). Unfortunately, only single specimens from Spain and the Canaries were available for study, but figure 9 shows that Blackcaps from all four regions are distinct, with the Spanish and Madeiran birds being almost as similar to each other as are the Canary and North African birds. If similarity reflects ancestry then Madeiran Blackcaps are related to the Iberian population, and Canarian ones are related to the North African. Even if the premise is accepted, it would not be justified to draw such conclusions when only single specimens from Spain and the Canaries were included in the analysis.

Firecrest (100%; greenness of back, crown colour, breast colour). Figure 10.

The Madeiran Firecrest (*Regulus ignicapillus madeirensis* Harcourt, 1851) is, to the European bird-watcher, distinct from the continental form, having brighter yellow 'shoulders' contrasting with a purer grey neck. These characters are more visible in the field than they are on museum specimens. DFA (figure 7) supports this feeling, showing *R.i.madeirensis* to be clearly separated from the other subspecies, with *R.i.teneriffae* Seebohm 1883 also distinct from the nominate and *R.i.balearicus* von Jordans 1924.

The museum skins of *R.i.madeirensis* confirmed the author's finding, whilst ringing in Madeira in 1981, that there is little or no sexual dimorphism in the crest colour in Madeiran Firecrests. Both sexes have crests of a colour intermediate between that of males and females of the nominate subspecies. Is this an example of the Island Syndrome mentioned in the introduction to this paper?

FIRECREST

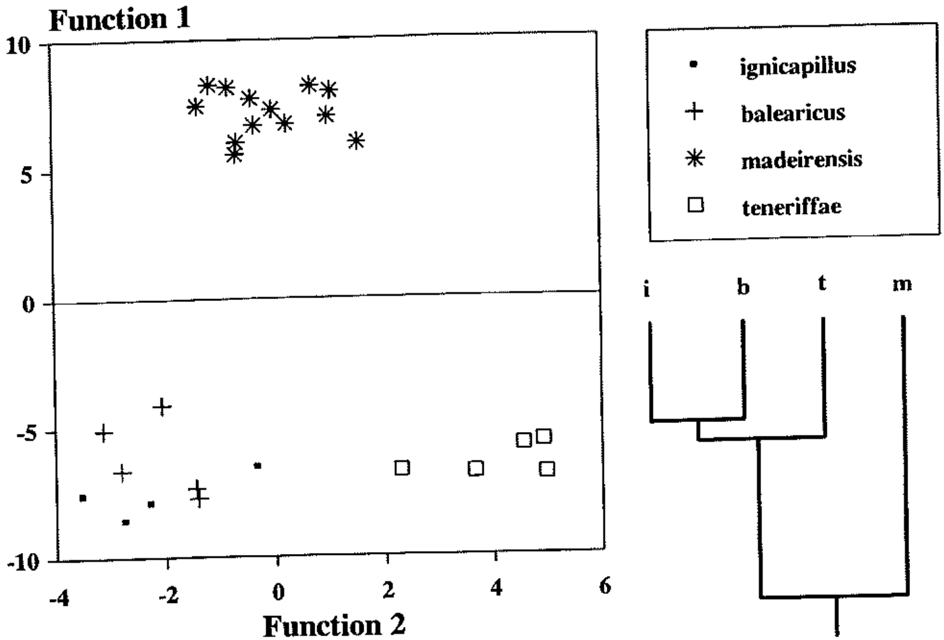

Figure 10. The first two functions discriminating between four sub-species of Firecrest (*Regulus ignicapillus*).

Rock Sparrow (81.25%; no other characters were scored). Figure 11.

The results of the analysis of the physical attributes of tree subspecies of Rock Sparrow are shown in figure 11. They indicate that birds from Madeira (*Petronia petronia madeirensis* Erlanger 1899) are more similar to those from continental Europe (*P.p.petronia* (L)) than to those from North Africa (*P.p.barbara* Erlanger 1899). Vaurie (1959) describes the Madeiran subspecies as 'somewhat darker', especially on the rump and crown, although 'the difference is but slight', and the North African subspecies as 'distinctly paler and greyer'. It was not possible to discern these differences on the skins examined.

ROCK SPARROW

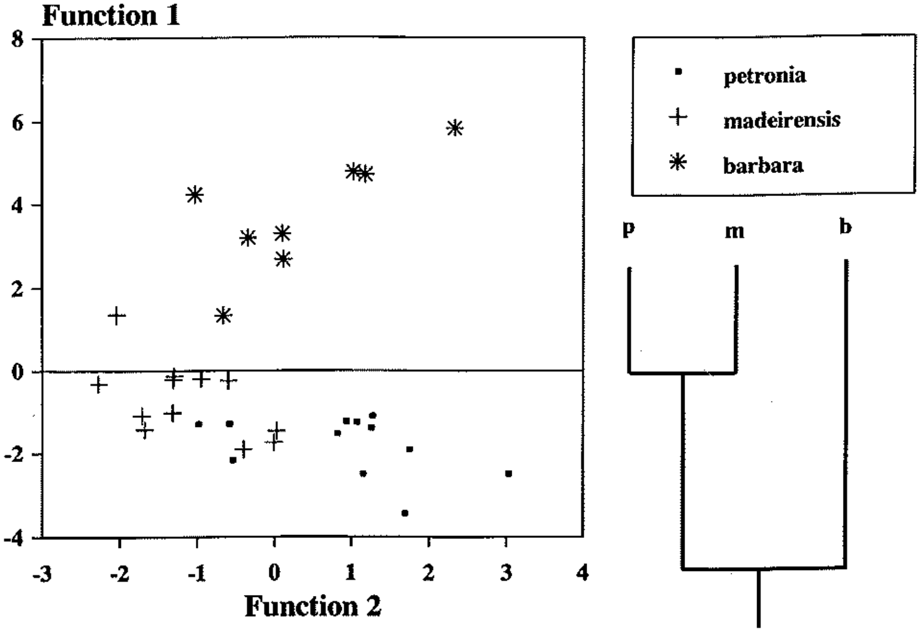

Figure 11. The first two functions discriminating between three populations of Rock Sparrow (*Petronia petronia*).

Chaffinch (100%; colour of back, rump, breast, cap, cheek, extent of white on tail). Figure 12.

The Chaffinches (*Fringilla coelebs* L) of the North Atlantic Islands form a complex assemblage of at least five subspecies:

F.c.moreletti Pucheran 1859 from the Azores
F.c.maderensis Sharpe 1888 from Madeira
F.c.tintillon Webb, Berthelot & Moquin-Tandon 1841 from Gran Canaria, Tenerife and La Gomera
F.c.palmae Tristram 1889 from La Palma
F.c.ombriosa Hartert 1913 from Hierro

CHAFFINCH

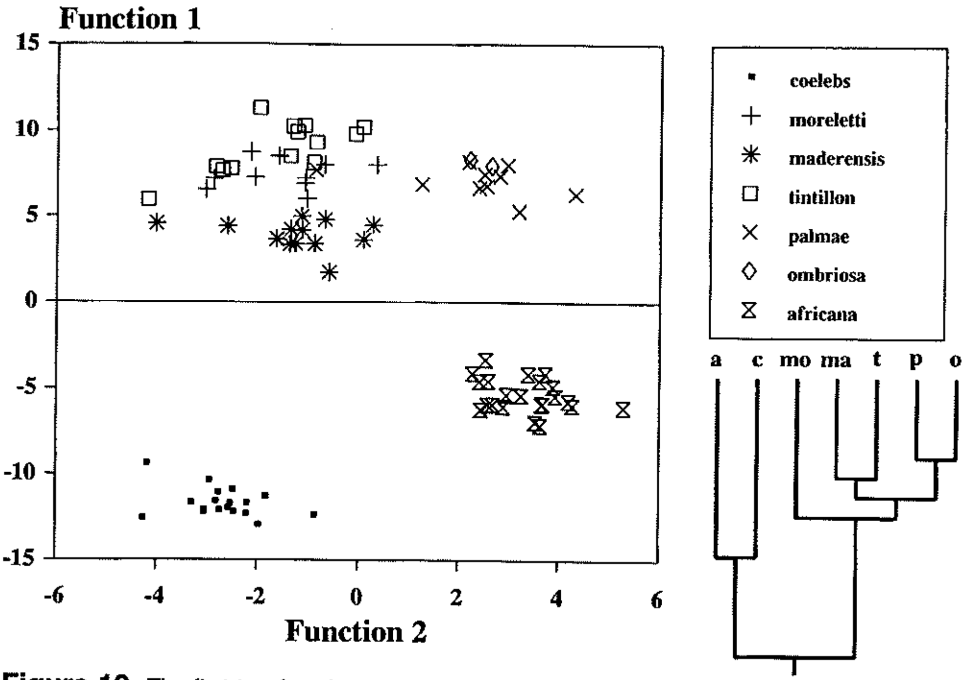

Figure 12. The first two functions discriminating between seven sub-species of Chaffinch (*Fringilla coelebs*).

There are two continental subspecies that could be related to these island forms: the nominate and the North African *F.c.africana* Levaillant 1850. Portuguese Chaffinches have been described as *F.c.iberiae* Harrison 1945, but are not widely accepted as being different from the nominate. Other subspecies have been described from Britain, and the Mediterranean.

The DFA clearly distinguishes between the continental (European and African) subspecies and the island ones, but is less clear about separating the latter into their component groups. Chaffinches from La Palma (*palmae*) and Hierro (*ombriosa*) are very similar, as are those from Madeira (*maderensis*) and the rest of the Canaries (*tintillon*). The Euclidian distances used to plot the dendrograms in figures 6 to 12 have been calculated from *all* the functions, not just the first two, which are illustrated, so that the crosses on the graph for *moreletti*, for instance, are on a different plane to that of the paper. By using all the functions, 100% of the specimens were correctly allocated by the DFA.

Unfortunately, this analysis does not shed much light on the origins of the various island subspecies - neither of the two continental subspecies being very close to any of the island ones.

DISCUSSION

Even for birds from such relatively well studied groups of islands as the Azores, Madeira, and the Canaries we still do not have enough biometric data for firm conclusions to be made about their differentiation and origins. Nevertheless, the analyses presented here permit some insights and tentative conclusions. There appear to be four levels of differentiation:

1) Some species are quite distinct, eg the pigeons

2) Chaffinches and Blackcaps are very different on each island, are distinct subspecies, and exhibit several of the characteristics of the Island Syndrome

3) Robins and Blackbirds are not as differentiated, but can be distinguished by discriminant function analysis

4) Firecrests, Canaries, and Rock Sparrows can be distinguished, but have not proceeded as far as the others in the direction of speciation.

Morphological (phenotypic) characters have always been used to distinguish taxa. While this may change with the advent of DNA hybridisation and fingerprinting, they are still the basis for most taxonomy. To use these characters, particularly biometric ones, to establish the possible origin of the various species one must accept that similarity is indicative of commonality of origin and, possibly, period of isolation. On the other hand, cladists claim that particular shared or unique characters should be used rather than overall similarity.

Madeiran Blackcaps and Blackbirds are most similar to European birds, whereas the Canary Island populations are most similar to North African ones (figures 8 and 9). Cladists would say that this, by itself, tells us nothing of their genetic affinities, and therefore, their origins. They would need evidence of *particular* shared characters before drawing such conclusions. Conventional taxonomists would take it that the Madeiran populations originated in Europe, whereas the Canary Island ones originated in Africa. Furthermore, they might be tempted to say that the four levels of differentiation (above) reflect the time during which each population has been present on the islands.

The debate between evolutionary taxonomists and cladists has been raging since the late 1960's, with no universally acknowledged winner. It may be that the biometric findings here reported would be supported by cladistic analysis - but that is another project.

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