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The numbers of bird species on islands

by David Lack

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ST. PATRICK EXPLICITLY banned snakes from Ireland, but the present state of the island suggests that his prejudices extended to woodpeckers, nightingales, and many other animals and plants. In all, only three-fifths of the land and freshwater birds that breed regularly in Britain breed regularly in Ireland (derived from Parslow 1967-68). Some other saints were more exclusive. St. Michael, for instance, allowed on his island in the Azores only about 21 native species, a tenth of the number in Iberia (derived from Bannerman 1966, Voous 1960), and St. Thomas permitted 33 on his island in the Gulf of Guinea, compared with 287 on Mount Cameroon (Amadon 1953, Eisentraut 1968).

These are just three examples of the fact that far fewer species of land birds reside on islands than the adjoining mainland. Most earlier workers assumed that this was due solely to difficulties of dispersal. However, Stresemann (1927-34) and Mayr (1940) showed that the number present is correlated with island-area, as demonstrated later in detail for the islands west of Sumatra by Ripley (1944), and for other types of animals on islands by Darlington (1957) and Preston (1962). But the degree of isolation is also important, and the clear need to combine the influence of the two factors led to the equilibrium theory of MacArthur and Wilson (1963, 1967): the distance of an island from other lands greatly influences the rate of colonisation of new species, while the size of the island greatly influences the rate of extinction of those present. Later, Hamilton and his co-workers (1964-67) showed for various other archipelagoes that the number of bird species on each island is closely linked with its size, and that its isolation is usually of minor importance, though the major factor in Darwin's finches in the Galapagos. They followed Ripley in considering that island-size is important because it reflects habitat-diversity, as well shown for the avifaunas of the Aegean islands by Watson (1964). In this lecture, I will discuss these problems in relation to the land (including freshwater) birds of various islands in the Atlantic, seabirds

being omitted. I hope to publish a fuller treatment later, but meanwhile the lists on which the present analyses are based have been deposited at the Edward Grey Institute. In such analyses, there are inevitably borderline decisions as to whether to include or exclude particular species, but their number is small and does not affect the conclusions reached.

Ireland

Ireland is nearest to home, so let us start there. Why should it have only three-fifths of the British breeding species? It is a typical 'continental' island, cut off from Wales in the first part of the last glacial period, when its flora, and presumably its birds, were arctic. The land link with Scotland persisted longer, but would have been unimportant for the spread of southern species. Hence most of its present birdlife presumably came across the sea. But Ireland is only 80 km. from Wales, which might be thought too short a distance to keep out any birds, except possibly woodpeckers. In fact, as shown in Table I over nine-tenths of the British breeding species which do not breed regularly in Ireland have been recorded there, and one-third of them have actually bred there occasionally or formerly. These latter species, at least, have not been kept out through failure to cross the sea. Even the Great Spotted Woodpecker *Dendrocopos major* has been recorded over fifty times, including twice in subfossil deposits, so may once have bred (Kennedy *et al.* 1954). Further, if the sea gap had been important, one would have expected migrants, with their stronger flight, to be proportionately better represented in the Irish avifauna than British residents, but the last two lines of Table 2 show the reverse. Finally, most of the British breeding species missing from Ireland do not breed so far west in Britain as the Irish Sea, so the latter cannot be the reason for their absence. The Welsh total of 122 breeding species (from Parslow 1967-68) is closer to the 102 for Ireland than the 171 for all Britain, though Wales is not separated by sea.

TABLE I—STATUS IN IRELAND OF 171 REGULAR BRITISH BREEDING SPECIES

Irish status		*number*	
breed regularly		102	
breed occasionally	have bred	19	24
once regular, now extinct	have bred	5	24
not breeding, but recorded		39	
never recorded		6	

NOTE:
Based on Kennedy *et al.* (1964) for Irish records, Parslow (1967-68) for British breeding species.

Presumably, therefore, two-fifths of the British avifauna are prevented from breeding in Ireland by ecological factors. Yet one's first impression is that Ireland 'looks just like Britain'. This is probably misleading, however, since, as compared with Britain, Ireland extends less far north and south, is wetter, with a cooler

summer and milder winter, and due to man, has far less woodland, while the surviving woods, with their evergreen understorey, are unlike most British oak woods. Moreover roughly two-fifths of the British flowering plants are absent (Praeger 1950).

In a few instances, the missing factor is obvious. Thus the absence of the Short-eared Owl *Asio flammeus* is linked with that of field voles *Microtus*, its normal prey, and the absence of the Red-backed Shrike *Lanius collurio* with the scarcity of warm and dry summer weather, which is needed by the large insects which form its main prey (Durango 1950). But for most other species, the missing factor is not known. What, for example, keeps out the Redstart *P. phoenicurus*, which is regular on passage in Ireland and has bred occasionally?

Indirect evidence suggests that, in at least most of the unexplained cases, the missing factor is ecological. As shown in Table II, the proportion of the regular British breeding species which breed in Ireland is over nine-tenths for those widespread in Britain, but only 42 per cent for those with a restricted British range which includes part of Scotland, and only one quarter for those restricted to the Scottish Highlands, while none breed of those restricted to England and/or Wales. It is reasonable to suppose that the species with a restricted British range have more specialised ecological requirements than the widespread species, and it is therefore less likely that the restricted than the widespread British species would find suitable conditions in Ireland. Moreover the biggest single group absent from Ireland are those which breed only in south or south-east England, where climate and ecology are least like those of Ireland; and at the other extreme, most of the Scottish Highland species are absent.

I got the idea for this analysis from the similar one on flowering plants by Praeger (1901, cited by Turill 1948). In plants, as in land birds, nearly all the species widespread in Britain occur in Ireland,

TABLE II—BREEDING RANGE IN BRITAIN IN RELATION TO PRESENCE IN IRELAND

British breeding range	*number of regular breeding species*		*proportion regular in Ireland*
	Britain	*Ireland*	
widespread	86	78	91%
widespread except S.E.	12	11	
widespread except N. Scotland	12	4	42%
only Scotland and N. England	7	4	
only N. Scotland	21	5	24%
only England and/or Wales	9	0	0
only S. or S.E. England	24	0	
TOTAL	171	102	60%
total residents	125	86	69%
total summer visitors	46	16	35%

NOTE: Based on Parslow (1967–68). Species which breed only occasionally in Britain are excluded; none of them breed in Ireland. No species breeds in Ireland but not Britain.

those least well represented are the ones restricted to eastern England. It may be added that in other land and freshwater animals, as in birds,' there are fewer species in Ireland than in Britain. In mammals, the proportion is 54 per cent, and the figure is the same for bats, which can fly, as for the other land or freshwater species (taken from Van Den Brink 1967, including long-established but not recent introductions). The proportion is similar, 53 per cent, for the regular butterflies (from South 1906 and Ford 1945), but only a quarter for the reptiles and amphibia combined, and as much as three-quarters for myriapods and four-fifths for molluscs (Praeger 1950).

The main lessons that I draw from Ireland are: (i) even a continental island 80 km. offshore has a much reduced avifauna, (ii) difficulties of dispersal over the sea are not responsible, (iii) a naturalist's first impression of ecological similarity can be highly misleading and (iv) the ecological factors presumably responsible are in most cases unknown, even though British birds are probably better known than those of any other country.

Iceland

Iceland lies just south of the arctic circle about 770 km. north of Britain and 930 km. west of Norway. As compared with the species breeding between similar latitudes in Norway, Iceland has 8 passerines (14 per cent), 6 other land birds (24 per cent), 10 wading and shore birds (44 per cent) and 23 freshwater species (100 per cent), while its 24 seabirds exceed the number in Norway (based on Gudmundsson n.d., Voous 1960). This disproportionate representation of Norwegian species accords with the ecological situation, as Iceland has no trees except small birches, no voles or lemmings, but fairly good marshes, abundant lakes and rich seas.

One owl, two ducks and three gulls colonised Iceland only in recent decades, which Gudmundsson (1951) attributed to the ameliorating summer climate, but while this may be one factor involved, gulls have been increasing throughout Europe, probably through foods incidentally provided by man, and the Short-eared Owl *Asio flammeus* presumably feeds in Iceland mainly on mice introduced by man. Another 7 species of birds have bred occasionally in Iceland in the present century, so at least these have not been excluded by the sea barrier but presumably by ecological deficiencies.

The Canary Islands

(a) *Compared with Madeira and the Azores*: Now let us move to the southern outpost of the European avifauna in the Canaries. As set out in Table III, the Canary Islands have 53 native land and freshwater bird species, just over a quarter of the number in Morocco (Bannerman 1963, Etchécopar and Hue 1967), but roughly twice as many as on Madeira or the Azores (Bannerman 1965, 1966). The Canaries consist of semi-desert, laurel forest with tree heath, pine forest, an alpine zone and much cultivation. Various of the absent Moroccan species would not find suitable

habitats there, and similarly the species restricted to semi-desert or pine forest in the Canaries are absent from Madeira and the Azores, which lack these natural habitats. But for the most part, the reasons for the absence of particular species are not obvious to superficial inspection. This might suggest that difficulties of dispersal are involved, but the Canaries are at their nearest only 100 km. from Africa, and 65 of the missing Moroccan species have been recorded there. Madeira and the Azores are much farther offshore, but 69 species which breed in Morocco but not Madeira have been recorded on Madeira, and 50 species which breed in Iberia but not the Azores have been recorded in the Azores, and this despite a paucity of local ornithologists (from Bannerman 1963-66). Hence difficulties of dispersal seem excluded for at least most birds.

TABLE III—THE CANARIES, MADEIRA AND AZORES

	Canaries	*Madeira*	*Azores*
distance from mainland (km.)	100	800	1400
approx. area (sq. km.)	7300	800	2400
number of species			
land and freshwater birds	53	27	22
butterflies	26	11	5
Coleoptera (omitting synanthropic)	990	565	180
Orthoptera	96	40	26
flowering plants	1531	*c.* 690	*c.* 610

NOTES: Distances and areas are rounded off as they are rather different in different works of reference. The numbers of resident bird species are from Bannerman (1963-6), omitting introduced and probably introduced species. The numbers of butterflies are from Baker (1891), Guichard (1967) and Rebel (1940), of Coleoptera from Uyttenboogaart (1946), and of Orthoptera from Chopard (1946). The numbers of plant species in the Canaries are from Lems (1960), and in Madeira and the Azores are the averages of the figures given by Tardieu-Blot (1946), Good (1947) and Williams (1964) respectively, which differ greatly, so are untrustworthy. The Cape Verde Islands have a mainly African, not European avifauna, but fit fairly well with the others. They have the second largest number of land and freshwater species of birds, are the second largest in area, the second nearest to the mainland, and have the second largest number of species of butterflies (Bannerman 1968); the totals for other insects and for plant species seem unreliable, but on present evidence seem too few in comparison with those on the other archipelagoes.

A comparison of these three groups of islands bears out two trends mentioned in the introduction. For the Canaries have the most bird species and are both the largest and the nearest to the mainland, and though the Azores are much larger than Madeira, they are much farther offshore, which helps to explain their smaller number of birds. But why, if difficulties of dispersal are not involved, should the most distant archipelago have the fewest species? Table III shows that the same holds in the three groups of insects which have been most fully collected, in all of which the Canaries have most and the Azores fewest species, and the same probably holds for the flowering plants, but published totals are unreliable. The numbers of plant and insect species presumably reflect the diversity both of habitats and of available foods for birds, so these findings fit the view that the numbers of bird

species are correlated with the ecological conditions. The question of why the remoter islands should have fewer plant and insect species, and hence a reduced ecological diversity, would take me outside the limits of this lecture.

(*b*) *Their broader niches*: Quite a number of the passerine and some other land birds in the Canaries, Madeira and Azores have broader habitats or feeding stations than on the mainland (Lack and Southern 1949, Buxton 1960, Marler and Boatman 1951, respectively). A case of special interest is the Blue Tit *P. caeruleus*, which is the only species in the genus *Parus* in the Canaries. There, it is common in both broadleaved and pine woods, though almost everywhere else restricted to broadleaved woods, and has a relatively long and thin beak (culmen 10.9 mm., depth 4.1 mm., *cf.* 10.1 × 4.1 mm. in North Africa, Snow 1953), so it has varied in the direction of the tits of conifers. I at one time supposed that it had expanded into pine forest because the Coal and Crested Tits *P. ater* and *P. cristatus* had failed to reach the Canaries. But many other instances are now known of one insular species with a broader niche or intermediate characters replacing two more specialised species which occur together elsewhere. I therefore suggest that, in the restricted ecological conditions on islands, one more generalised species is liable to oust two specialists, a point discussed for animals in general by MacArthur and Levins (1967). This tendency provides a minor reason for the reduced number of species on islands.

Similarly, while in Morocco the Rock Sparrow *P. petronia* lives in the countryside and is replaced by a species of *Passer* in the towns, the Rock Sparrow was formerly the only sparrow in the Canaries, where it lived in both the countryside and the towns. But the Spanish Sparrow *Passer hispaniolensis* colonised Gran Canaria from the eastern Canaries in the mid-nineteeth century, and, after failing on Tenerife in the 1880s, re-established itself about 1900, and fifty years later it started breeding on the western Canaries, and yet later on Madeira, in each island displacing the Rock Sparrow from the towns, though not the countryside (Bannerman 1963, 1965). This might suggest that the Rock Sparrow was formerly in the towns of the Canaries simply because the Spanish Sparrow had failed to reach them. But in view of its slow spread between Canarian islands only 60 km. or less apart, and of its first failure on Tenerife, I now think it more likely that there was not 'ecological room' in the Canaries for both species until the towns reached a certain size, before which the more generalised Rock Sparrow could exclude the Spanish Sparrow. The Spanish Sparrow has similarly displaced *Passer iagoensis* from the towns but not the countryside of the Cape Verdes in recent times (Bannerman 1968).

While the Canaries and Madeira have the Firecrest *Regulus ignicapillus*, the Azores have the Goldcrest *R. regulus*, and these two species are so similar that the difference is perhaps due to the chance of which of them arrived first, after which it became adapted to the local conditions and could exclude the other.

(c) *Variations within the Canaries*: The number of bird species on each of the main Canary Islands is set out in Table 4. As the greatest distance between neighbouring islands is only 80 km., dispersal between them should be easy, and in fact the most isolated islands, La Palma, Hierro and Gran Canaria, do not, on average, have fewer species than the rest. The larger islands tend to have more bird species (Hemmingsen 1963). However, though Fuerteventura is the second largest island, it has rather few species, probably because it consists of only one main habitat, semi-desert. Hence the correlation between bird species and island-area is probably due to the correlation between the latter and habitat-diversity. The direct influence of habitat is seen in the absence of semi-desert species from Gomera, Hierro and La Palma, which lack this habitat, and by the restriction of pine-forest species to the only islands, Gran Canaria and Tenerife, with extensive pine forest. But most other absences cannot be explained by the absence of main habitats. As shown in Table IV, however, the number of species of birds is correlated with those of both flowering plants and butterflies (the only other groups for which I have found figures), and this indicates that ecological factors are involved.

TABLE IV—NUMBERS OF SPECIES ON MAIN CANARY ISLANDS

	area (sq. km.)	*altitude (m.)*	*habitat diversity*	*number of species*		
				birds	*vascular plants*	*butterflies*
Lanzarote	870	670	1	31	370	9
Fuerteventura	1730	810	1	33	350	10
Gran Canaria	1530	1950	4	44	760	18
Tenerife	2060	3710	4	45	1080	24
Gomera	380	1480	1	36	540	20
Hierro	280	1520	1	32	390	12
La Palma	730	2420	2	36	580	20

NOTES: Numbers of bird species based on Volsoe (1951, 1955), Bannerman (1963) and Hemmingsen (1963), of vascular plants on Lems (1960) and of butterflies on Guichard (1967). For habitat diversity, one point is scored for the presence of each of semi-desert, laurel forest, pine forest, alpine zone and lagoons. The most isolated islands are Hierro and La Palma, some 60 km. from the next island to the east, with no islands farther west; the next most isolated is Gran Canaria, some 80 km. from Fuerteventura and 60 from Tenerife.

The most puzzling case is the Chough *P. pyrrhocorax*, which is common in both natural and cultivated habitats on the western-most island of La Palma, but absent from all the other islands, some of which are in clear view one hour's flight away and appear to provide similar conditions. Yet attempts to introduce the Chough on Tenerife failed (Bannerman 1963). Presumably there is an unrecognised ecological deficiency, and if you think this unlikely, I would ask you what similarly restricts the Chough to western Britain, where a sea barrier is not in question?

La Palma has pine forest, but neither of the two Canarian species restricted to this habitat, the Great Spotted Woodpecker or Blue Chaffinch *Fringilla teydea*, occurs there, presumably because the pines occupy too small an area. The form of the Common Chaffinch *F. coelebs* on Palma lives in both broadleaved woods

and pines, whereas that on Gran Canaria and Tenerife is restricted to broadleaved woods and the Blue Chaffinch is in the pines. Hence this is another example of one species with a broader niche on a smaller island replacing two found elsewhere, and the Palman Chaffinch is intermediate between the other two in both dimensions and colour (see Table V). It should be stressed that the habitat of the Blue Chaffinch is not absent from La Palma, but merely occupies a smaller area than on the islands where it occurs.

TABLE V—DIFFERENCES IN CHAFFINCHES *Fringilla* SPP. IN CANARY ISLANDS

	F. coelebs		*F. teydea*
	Gran Canaria and Tenerife	*La Palma*	*Gran Canaria, Tenerife*
habitat	broadleaved	broadleaved and pine	pine
underparts	rufous	pink chest, white abdomen	white
♂ winglength (mm.)	83	87	94, 104
culmen (mm.)	14.5	14.9	15.5, 18.3

NOTE: Measurements are the middle positions between the extremes given by Volsoe (1955, p. 136). There is a general tendency, *e.g.* in tits *Parus* and nuthatches *Sitta*, for the species in conifers to have proportionately longer and thinner beaks and paler underparts than their congeners in broadleaved woods, and the chaffinches follow this, presumably adaptive, trend.

(*d*) *Lessons to be drawn*: (i) The number of resident bird species is correlated with island area, but is lower than expected on these grounds in the Azores, which are remote, and on Fuerteventura, which has a restricted habitat. (ii) Many more species have occurred than breed, so difficulties of dispersal are probably not involved, even on the Azores. (iii) Hence the number of bird species is probably determined by ecological factors, and fitting with this, it is strongly correlated with the numbers of plant and insect species. (iv) In several instances, one species with a broader niche replaces two specialists elsewhere, probably as a result of competitive displacement in restricted ecological conditions.

The Guinea islands

Details for the four islands in the Gulf of Guinea are shown in Table VI. Fernando Po was connected with the mainland until the last few thousand years, the others are oceanic. Although Fernando Po is only 32 km. offshore, it has just under half the number of species found on Mount Cameroon (Eisentraut 1965, 1968), a

TABLE VI—THE ISLANDS IN THE GULF OF GUINEA

	Fernando Po	*Principe*	*Saó Tome*	*Annobon*
distance from African mainland (km.)	32	220	280	340
distance from next island to north (km.)	—	220	146	180
area (sq. km.)	2000	126	1000	15
altitude (m.)	2850	948	2024	655
indigenous flowering plants	826	276	556	115
native land and freshwater birds	138	23	36	8

NOTES: Based on Eisentraut (1963, 1968), Amadon (1953) and Fry (1961) for the birds, and Exell (1944) for the plants.

bigger reduction than that between Ireland and Britain, where the sea-gap is twice as wide.

The number of bird species on each of the Guinea islands is strongly correlated with area and to a smaller extent with distance offshore (Hamilton and Armstrong 1965). Sao Tome has fewer species relative to either Fernando Po or Principe than would be expected from their respective areas, and this may be linked with its being farther offshore. Yet it is hard to believe that distances of up to 280 km. have prevented so many African species from colonising. The number of bird species is also correlated with the number of plant species, so perhaps the influence of distance offshore on the birds is secondary, and due to its influence on the number of plant species, and hence on the diversity of habitats and foods.

Principe and Sao Tome are Tertiary volcanoes with fertile soils and similar-looking forest, except that Principe has only lowland forest, whereas Sao Tome has both lowland and highland forest (Exell 1944). Although they are only 146 km. apart, the difference in their avifaunas 'is like the crossing of a major zoogeographical boundary' (Snow 1950). Considering geographically replacing species in the same superspecies to be the same, and omitting probable human introductions, 7 of the 23 native land birds on Principe and 20 of the 36 on Sao Tome are not found on the other island. Indeed, 5 of the 7 on Principe are in different genera from any on Sao Tome, as are 16 of the 20 on Sao Tome but not Principe, and several of them are in different families. Some of them are so different that the ecological resources must be exploited in different patterns on the two islands. There has, however, been some avifaunal interchange, as they share four endemic species and one endemic genus (Amadon 1953).

It is tempting to attribute the start of these differences between the two avifaunas to the chance of which bird species arrived first, but even if this is correct, their continuance is presumably due to competitive exclusion, the species present having evolved into a closely interlocked ecological group which makes it hard for further species from the other island or the mainland to become established. Moreover, though the climate of the two islands is similar and their forests look alike, they differ botanically to an important extent. Of the 276 species of flowering plants on Principe, 33 per cent are not found on Sao Tome, and even when endemic species in the same genus are equated, as being essentially similar, the proportion is 27 per cent. Likewise 64 per cent of the species of flowering plants on Sao Tome are not on Principe (derived from Exell 1944). In part, therefore, the bird species on the two islands might be different because the ecological conditions are different.

Annobon, 15 sq. km. in area, has 8 resident bird species, only two of which are passerines, which must be near to the minimum for a tropical forest. One, the endemic white-eye *Zosterops griseovirescens*, is intermediate in size between the two species of white-eyes on the other island (wing 62 mm., culmen 15.8 mm., *cf.* (i) 55 and 12.7 mm., (ii) 74 and 15.9 mm. for the two species

on Sao Tome (Moreau 1957). This is another example of two species on larger islands being replaced by one intermediate species on a smaller and more remote island.

Hence the birds of the Guinea islands illustrate many of the earlier lessons. They also show that two adjoining and similar-looking islands may have very different avifaunas, but it is uncertain to what extent this is due to differences respectively in their vegetation, or in which mainland bird species happened to arrive first. In either case, the persistence of such differences is most reasonably attributed to competitive exclusion.

Puerto Rico and Jamaica

The number of bird species on each of the main West Indian islands is correlated with area (Preston 1962), but this point need not be documented further, and I wish to make two others, concerning passerines and hummingbirds respectively. Both Puerto Rico and Jamaica include semi-arid lowland scrub forest and montane rain forest, but former rich lowland forest has been replaced by cultivation, largely of sugar. Puerto Rico, nearly 9,000 sq. km. in area, has 26 native passerine species, and Jamaica, which is one-third as large again, 35 species. What most struck me in June 1969 was that, in two days in the field on Puerto Rico and three on Jamaica, without making special efforts to find new birds I saw 87 per cent of these species, a far higher proportion than would have been possible of the much greater number in mainland tropical forest. Evidently most of the island birds are widespread and plentiful.

On the basis of censuses of standard areas, MacArthur, Recher and Condy (1966) showed mathematically that the number of species present per feeding layer is similar in Puerto Rican and Panamanian forest, provided that the Puerto Rican forest is held to consist of two layers (ground and trees) and the Panamanian of four (ground, shrubs, and two heights of trees). Probably, therefore, the reduced number of island species is linked with their subdividing the vertical feeding zones to a smaller extent than the mainland species do, but this has not been checked by observations on their feeding stations. The same workers also showed that an increase in the size of their census areas led to more species being included in Panama but not on Puerto Rico, suggesting that the island species occupy wider habitats than those in Panama.

To test the latter point, I compared the habitats of the forest birds on Puerto Rico and Jamaica (based on Bond 1960), with those for the only mainland area of tropical forest for which such data have been published, Usambara in Tanzania (Moreau 1948). Of 35 passerine species and 17 other land birds in the families cuckoos to woodpeckers inclusive, 54 per cent are found in both arid lowland forest and highland rain forest. In contrast, of the 60 rain-forest birds analysed in Usambara, only 8 per cent are common to both lowlands and highlands; also one-third of these are restricted to forest edge, as compared with only 7 per cent of the West Indian species. Further, another 30 lowland species in Usambara are in one (but no more) of three more arid wooded habitats,

riverine forest, wooded grassland or semi-desert thorn trees, and none of these species are in rain forest. Clearly, the island species have much wider habitats than those of tropical mainland.

Hence the point illustrated in earlier sections, that one island species with a broader habitat or ecological niche may replace two mainland specialists, is just a small part of a general trend for islands to have fewer species with broader habitats or niches than the mainland. As mentioned earlier, the reduced number of species on islands was formerly attributed to difficulties of dispersal, from which it would follow that the species present evolved broader niches because many of their mainland associates are absent. But since dispersal to islands is much more frequent than once thought, I suggest that cause and effect are the other way round, that the reduced flora and insect fauna on islands provide conditions such that bird species with broader niches tend to exclude more specialised species, and that this has caused the reduction in the numbers of species.

Each of the main West Indian islands has one small species of hummingbird, belonging to one of 4 different genera, and usually two larger species belonging, respectively, to 2 out of 6 other genera. Hence there is considerable replacement on different islands by species in different genera. This situation might have arisen through the chance of which mainland species reached each island first, but even if it did, it is presumably maintained today by competitive exclusion, since otherwise one could hardly expect each island to have just three of the available 10 genera. This view is supported by the exceptional situation on Puerto Rico, the main part of which has three species, whereas the Virgin Islands to the east have two in different genera. This sort of situation occurs elsewhere; the exceptional point is that the extreme east of Puerto Rico has the same two species as the Virgins and not those on the rest of Puerto Rico. As there is no sea gap or other geographical barrier, competitive exclusion must be involved and, if here, then presumably also in the parallel cases involving separate islands. It may be added that while nearly all the main islands have three species, Cuba has only two, while Dominica and Martinique have four, the reasons for which are not known.

My main inference from the West Indies is that the relatively few forest birds have much broader ecological niches, in both horizontal and vertical planes, than those on the mainland, that this is because the reduced ecological diversity enables fewer species with broader niches to displace more species with narrower niches, and that this is a major cause of the reduced avifauna. That most islands have only 3 (out of 10) genera of hummingbirds presumably has a similar explanation; that these are different on different islands might have originated through the chances of colonisation, but is maintained (if it was not initiated) by competitive exclusion.

The Tristan group

The most isolated islands in the Atlantic, indeed in the world, are the Tristan group, 2,800 km. from South Africa and 3,200 km.

from South America, whence their land birds were derived. Since there are at most only four species of land birds on any one island, and only two species on Gough, 350 km. away, one might think that, here at least, difficulties of dispersal have been of primary importance. However, 9 further vagrant species were recorded in two years on Tristan (Elliott 1957) and 6 in three recent weeks on Gough (C. Elliott *pers. comm.*), and these must be a tiny fraction of those arriving during the last few thousand years which failed to establish themselves. Islands of 135 and 100 sq. km. respectively near a continent would, however, have had many more resident species of birds than Tristan or Gough. Hence their great isolation must be an important factor, but its influence has presumably been secondary, through its effect on the plants and insects. Thus there are only 38 native species of angiosperms on Tristan and 35 on Gough (Wace and Dickson 1965, modified by Wace *pers. comm.*), hence the foods and niches available on these islands for birds must be few.

Three endemic passerines, a thrush *Nesocichla* and a larger and smaller finch *Nesospiza*, coexist in the Tristan group. Another finch, *Rowettia*, is the sole passerine on Gough, where it occurs in all the land habitats and also feeds below the hightide line, eating grass seeds, berries and other fruits, adult diptera, moth larvae, spiders, amphipods, vertebrate carrion, and food provided by visiting scientists (M. K. Swales *pers. comm.*). It would seem the ultimate 'all-purpose bird', and to fill on Gough the niches of the Tristan finches and thrush (not solely of the thrush, as suggested by Elliott 1957). Once again, therefore, one species on a remote island replaces two or three more specialised ones elsewhere.

Some islands outside the Atlantic

A few comments on islands outside the Atlantic strengthen the points made here. The number of species of Darwin's finches on each Galapagos island is closely correlated with its distance from the other islands (Hamilton *et al.* 1967). But the reasons for this correlation are ecological, since the *Geospiza* species often cross the 50-130 km. gaps between the islands, and the numbers of resident species can be explained in terms of habitat diversity, combined with a tendency for one intermediate species to replace two more specialised ones on small or outlying islands (Lack 1969). Again, Cocos Island, 520 km. southwest of Costa Rica, has only 4 resident species of land birds, but this can hardly be attributed to difficulties of dispersal, since another 23 species were seen there in 9½ weeks (Slud 1967).

Each of the largest Caroline Islands, Ponape and Palau, has three species of white-eyes, the small *Zosterops conspicillata* (wing *c.* 55 mm.), the medium *Z. cinerea* (*c.* 63 mm.) and a specis of the large *Rukia or Megazosterops* (71-82 mm.). The smaller islands of Yap and Truk have only the small and the large species, while remote Kusaie has only the medium species (Mees 1969). If, with more limited resources, two species displace three, one would expect the medium species to be the one excluded, and if resources

are yet more limited, so that only one can survive, one would expect the medium species to have the advantage. Hence this situation fits well with the view that the number of species is determined by the ecological resources.

In the last hundred years, 10 Australian species have established themselves in New Zealand, 1,600 km. away (Fleming 1962, Falla *et. al.* 1966). This rate of dispersal may be usual, but the rate of establishment is exceptionally high, and was presumably made possible by the great modification of habitats by man. This also accounts for the success of the many alien species introduced by man to New Zealand or Hawaii.

Finally, may I add a case from mammals? When Reindeer *Rangifer tarandus* were introduced to St. Matthew Island in the Bering Sea, they increased and flourished for just over twenty years, by which time they had eaten out their food supplies beyond the capacity of the plants to reproduce themselves and became extinct (Klein 1968). Here, then, is another instance in which a superficial ecological impression of the suitability of an area is misleading.

CONCLUSIONS

Far fewer bird species live on an island than on an equivalent area of adjoining mainland, even when the mainland is close (32 km. from Fernando Po). The number present tends to be correlated inversely with the distance from other land, but birds often cross wide seas (*e.g.* to Tristan da Cunha), even in the tropics (*e.g.* to Cocos), so difficulties of dispersal are unimportant. The only other reasonable explanation is that ecological conditions are restricted on islands. This fits the widespread correlation between the number of bird species and island-size, since island-size is correlated with habitat-diversity. It also fits the correlation between the numbers of bird and plant or insect species on islands (*e.g.* in the Canaries, Madeira, Azores and Guinea islands).

Some species are excluded from islands by the absence of their habitats (forest birds from Iceland, desert or pine forest birds from some of the Canaries, various of Darwin's finches from outlying Galapagos islands) and others by the absence of their normal prey (rodent predators from Iceland). But such obvious deficiencies do not account for most bird absentees, and it has to be presumed that many ecological restrictions are not obvious (*e.g.* for the Redstart in Ireland or the Chough in the Canaries). That such restrictions exist is shown by the frequency with which newcomers breed occasionally on islands without persisting (*e.g.* in Ireland or Iceland) and the paucity of such records from most other islands may well be due to lack of observations. Occasionally the ecological deficiency is due to a long-term interaction (the Reindeer on St. Matthew).

On a small or remote island, one species of intermediate characters or ecology at times replaces two more specialised species present elsewhere (*e.g.* Canarian Blue Tit, Canarian Rock Sparrow, Palman Chaffinch, Annobon white-eye, Kusaie white-eye and several

of Darwin's finches), or two may replace three (Caroline Islands white-eyes). This is presumably because, where the ecological resources are limited, a generalised species tends to exclude two specialists, and it provides a minor reason for the reduced number of bird species on islands. More important, it is a small part of a general tendency for land birds on islands to have broader habitats and feeding stations (*e.g.* in the Canaries, Madeira, Puerto Rico and Jamaica), which I likewise attribute to the reduced ecological diversity, and which I conclude is the major factor reducing the number of bird species on islands. (This is alternative to an earlier view that birds have broader niches on islands because many mainland species have failed to reach them.)

I therefore consider that, so far as land birds are concerned, islands are ecologically stable, which is contrary to the high rates of extinction and fresh colonisation postulated by Mayr (1965) and implied in the MacArthur-Wilson curves. But I hold this view solely for primaeval habitats, and where man has replaced them by cultivated land, there may be many temporary ecological vacancies, which might account for the success of many land birds self-introduced or introduced by man to New Zealand. The rapid turnover of species on many islands in recent times need not be regarded as typical of islands in a natural state.

Although I hold that islands are ecologically stable, each island need not be filled by the same species, as shown by the different species of goldcrests in the Azores and Madeira, the different genera of hummingbirds in certain West Indian islands and the different 'avifaunas' on Principe and Sao Tome, where the ecological resources must be divided differently. Such differences might have arisen through the chances of colonisation, but even if they did, they are presumably reinforced by competitive exclusion at the present time (as shown particularly by the hummingbirds on Puerto Rico). Several authors have argued, and I agree, that the first-comers to islands have an advantage, because they evolve adaptations to the local conditions, after which they are likely to exclude later arrivals. If, as argued here, dispersal to islands is much more frequent than supposed formerly, it follows that the first-comers evolve their differences very quickly; but recent research indicates that subspeciation can likewise occur much faster than once supposed.

This raises a final question about island endemics. The proportion of endemic subspecies on the islands discussed here is 3 per cent in Ireland, 21 per cent in Iceland, 30 per cent in the Azores and 45 per cent in the Canaries (from Vaurie 1959, 1965); yet the Canaries are much closer to the mainland than are the Azores. Again, the figure is 3 to 5 per cent on Zanzibar and Pemba (Moreau 1966) but 30 per cent on Fernando Po (Eisentraut 1965, 1968), which is a similar distance offshore. Finally, on Principe and Sao Tome, respectively 61 and 67 per cent of the resident birds are endemic, many at the specific and three at the generic level (Amadon 1953).

Clearly, the distance of an island from the mainland or other

islands is not the sole factor influencing the degree of endemism. Some of the above anomalies are explained on the assumption that forest birds disperse much less readily than those of open country; in particular there are many more forest species on Fernando Po than Zanzibar. But this is not the whole story. Moreover the evidence in this lecture shows that dispersal to islands is far more frequent than once supposed. I therefore suggest that the degree of endemism on an island is influenced not only by its isolation, which reduces the likelihood of the island populations meeting others, but also by its ecological peculiarities, which favour the evolution of adaptive differences and make interbreeding with individuals from other populations disadvantageous.

Sometimes endemism is high even on near-by islands. In the Solomons, for instance, endemic subspecies of white-eyes *Zosterops* are separated by straits 2 km. wide, and full species by straits 5 km. wide (Mayr 1942). Birds can fly such distances in a few minutes, but if the differences between these forms are adapted to the local conditions, there will be strong selection in favour of each individual keeping to its own island. Probably the sedentariness of insular forest birds is at least as much a result as a cause of their endemism. As Mayr once remarked, birds can use their wings to stay where they are.

My general conclusion, then, is that the small numbers of resident bird species on islands are due, not to difficulties of bird dispersal, but to ecological limitations, to which the island birds are often specially adapted, and which enable fewer species with broader niches to exclude a greater number of specialists. The degree of ecological impoverishment, including the number of plant species, is correlated with both island-area and isolation and so, therefore, is the number of bird species, but why the degree of ecological impoverishment (from the avian standpoint) is correlated with isolation is outside my present subject.

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