MIGRATORY BIRDS OF RELICT DISTRIBUTION: SOME INFERENCES

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To determine why one species, genus, or family has been replaced by another during the course of evolution is a problem at once important and difficult. The study of this question led the writer to investigate migratory birds of relict distribution. The results, though tentative, seemed so interesting that they are summarized here. The following species will serve as a basis for the later discussion.

1. Ross's Goose (*Chen rossii*).—This diminutive goose, whose total present population is thought to be less than 5,000 individuals, breeds only in a relatively small area in the Perry River district of the Canadian Arctic. In late or cold summers, as found by Peter Scott and H. C. Hanson, only a fraction of the total population may succeed in nesting, or even attempt to nest. The winter range is equally circumscribed, and comprises only the interior valleys of California.

2. Labrador Duck (*Camptorhynchus labradorius*).—This extinct species is believed to have nested on the coast of Labrador. It wintered coastally in the area from the Maritime Provinces to Chesapeake Bay. The Labrador Duck is apparently the *only* bird whose range was restricted to the American coast of the North Atlantic. The other coastal species of this area nest also in northwestern Europe, in Iceland, or in other areas. (The Ipswich Sparrow [*Passerculus princeps*] is an exception to this statement, but it is merely an insular race or representative of the widespread Savannah Sparrow [*P. sandwichensis*]).

3. Whooping Crane (*Grus americana*).—The Whooping Crane has revealed how a species, even one possessing great powers of flight and of migratory habits, may become restricted, in a comparatively short time, to very limited nesting and wintering areas. The nesting range of this crane once covered a vast area in the center of the North American continent from the far north, south to Iowa or even Louisiana. The breeding range of the few remaining pairs was for some years a mystery, despite the conspicuousness of this huge white bird, but is now believed, on the basis of one or two individuals observed in the summer of 1952, to be in the marshes adjoining Great Slave Lake. Its winter range is at present almost confined to the Aransas Wildlife Refuge on the Gulf coast of Texas. A few may winter elsewhere, as there is recent sight record of a pair in Tamaulipas, Mexico (Evenden, 1952).

The small size of both the winter and summer ranges of the Whooping Crane may, it must be admitted, be determined by its gregarious habits. We cannot safely assume that the areas where it is now found are more favorable than any existing elsewhere.

4. Bristle-thighed Curlew (*Numenius tahitiensis*).—This shorebird was discovered on Tahiti by one of Captain Cook's Expeditions. It is now known to winter on this and numerous other small islands in the mid Pacific, and nowhere else (Stickney, 1943). It was believed to be resident in Polynesia, until specimens were collected in Alaska, and it was correctly assumed that the breeding range was there. Not until a few years ago, however, was the first nest actually discovered by Allen and Kyllingstad (1949). These naturalists state that the dry upland tundra east of the Alaska coastal range, where *Numenius tahitiensis* nests, is barren and almost devoid of other breeding birds. West of the coastal range, in the low, well-watered tundra near the sea, numerous species of shorebirds and waterfowl nest in abundance. Among them are a few that might compete with the Bristle-thighed Curlew, notably the Whimbrel or Hudsonian Curlew (*Numenius phaeopus*), and perhaps in former days the Eskimo Curlew (*Numenius borealis*).

The migration of the Bristle-thighed Curlew involves a trans-oceanic flight, presumably non-stop, of over 2,000 miles from Alaska to the Hawaiian Islands, the nearest area where it winters. Since few are recorded in Hawaii, most of them probably fly on to islands still farther from Alaska.

There is not a single record of this curlew from Canada or the United States. This is ample proof that its remarkable migratory behavior is firmly established.

5. Slender-billed Curlew (*Numenius tenuirostris*).—This Eurasian curlew is, according to Stresemann and Grote (1943), threatened with extinction. It breeds in western Siberia and migrates far to the west to winter in the countries bordering the Mediterranean. Some individuals do, however, winter at intermediate points in Persia. Although a considerable number of Asiatic bird species migrate southwest to winter in Africa, there seem to be few, if any, others that fly west to winter in the Mediterranean area. The rather restricted breeding range is also unusual, though matched by some other Asiatic scolopacids, which, however, may, along with *tenuirostris*, all be relicts.

6. Bachman's Warbler (*Vermivora bachmani*).—This warbler nests very locally from Missouri to South Carolina but is extremely rare. Years have passed without a single one being recorded. Its ecological requirements are probably very stringent. Bachman's Warbler

winters in a restricted, insular area, Cuba and the Isle of Pines. Perhaps it was a relict species before the advent of white man—though apparently it was less rare a generation ago than at present.

7. Kirtland's Warbler (*Dendroica kirtlandii*).—The Jack Pine Warbler, as this species is also called, nests only in a few counties in central Michigan and even there is restricted to burned-over areas in which the new growth of jack pines is within certain limits of size. Thus severely limited ecologically, its population is not a large one—the total number was estimated to be less than 1,000 birds (Mayfield, 1953).

The winter range of the Kirtland's Warbler is the Bahama Islands—(map: Van Tyne, 1951). Although there is some pine country in the Bahamas, this is said *not* to be the habitat frequented by this warbler during the winter. Van Tyne and Mayfield, on a recent winter trip to the Bahamas made with the specific intent of studying Kirtland's Warbler, failed to record a single individual. This suggests that the winter habitat is not at present fully occupied. The same, however, may be true for the nesting grounds, for there are stands of pine in adjacent areas, for example in central Wisconsin, which, superficially at least, appear suitable for the species.

WHAT ARE RELICT SPECIES?

There are several types of biological "relicts," as Simpson (1944: 144–147) and others have shown. For present purposes we may regard as a relict species one whose numbers or range or both have undergone drastic reductions. With birds we usually lack fossil evidence to prove reduction of range, though the California Condor (*Gymnogyps californianus*) and a few others provide exceptions. When a species occupies a very limited area on a continent or has a very local or discontinuous distribution, we may suspect that it is a relict. This is especially true when it is well set off taxonomically and is not a geographical representative of any species. Some species of narrow geographical distribution, especially those found on islands or mountain peaks, may be just the opposite of relicts, that is, they may be of recent evolution. Such forms will not, as a rule, be limited to a small area on a continent in the absence of pronounced physical barriers.

Relict species survive in areas where competition is least severe. This may often be an island, merely because, by chance, more agressive forms did not happen to reach the island. Lemurs, for example, are still common and varied on Madagascar; elsewhere they have been largely displaced by the higher primates, which never reached Madagascar.

On continents, relicts often survive by becoming more and more specialized, through a process of natural selection, to a narrow ecological niche where they do manage to retain a competitive advantage. Hutchinson (1951) has found evidence to suggest a fugitive type of survival in certain fresh-water invertebrates. These species spread quickly into new bodies of water where they flourish, only to be displaced by species arriving later. This type of relict survival might evolve in birds. Moreau (1952) has found that certain winter migrants to Africa live in flocks which apparently travel great distances in search of areas where unusually heavy rains or other local conditions have produced a superabundance of food. The adaptation is thus analogous to that postulated by Hutchinson. Wynne-Edwards (1952) concluded that under arctic conditions adaptation may be primarily to allow a species to take advantage of temporarily favorable conditions or to recuperate from blows of the physical environment. Under such circumstances interspecific competition, even between exceedingly similar species such as the two redpolls of the genus *Acanthis*, may not, he believes, be of great importance.

The specialized niches in which relict forms survive often appear deficient or submarginal, but this is a relative matter. If the Bristle-thighed Curlew can nest successfully only on dry, barren tundra, then this habitat is, despite its shortcomings, optimum for this bird. On its winter home on Pacific atolls, the curlew supplements its diet with tern eggs, suggesting that the available food supply is not ideal for a shorebird. Again, however, the fact that it does winter successfully in Polynesia and not elsewhere is sufficient evidence that this is now the best area for it. Meinertzhagen (1928) has spoken of the fauna of the Tibetan Plateau as composed to a large extent of relict forms that have retreated to this bleak area, "whither their enemies have not been able to follow." The concept is, I believe, a valid one, but we must bear in mind that the "strategic retreat" of such forms is a long-term, involuntary, selective process. Dr. A. E. Parr has suggested to me that many deep sea fishes may be relicts of this type.

COMPARISON OF RELICT AND DOMINANT SPECIES

Relicts are species that tend to become more and more restricted both geographically and ecologically, because they are unable to compete successfully with other species. At the other extreme are those dominant or ultra-successful species that are expanding geographically and also, in many cases, in ecological tolerance. The American Robin (*Turdus migratorius*) is an example. Its breeding range is enlarging in the southeast and also in the far west. Its tendency to push into

new ecological niches is shown by the number of nests which it builds in more or less unsuitable places. At first glance it is often difficult to see why such a species is so numerous in spite of the high nesting mortality. Actually, the mere existence of numerous "submarginal" nests is an indication of aggressiveness and adaptability.

In an important paper on the ecology of Swedish birds, Svärdson (1949) showed that a species may, so to speak, behave like a relict one season and a dominant the next. When a cyclic bird is abundant it overflows from its optimum adaptive niche into all sorts of habitats in which it is not usually found and in which it is not very successful. When its population is at a low ebb, on the other hand, it is to be sought only in the most "typical" habitat. Relict forms are, from this point of view, ones that have been forced permanently into specialized little niches. Sometimes this means that they are found only in one small breeding area, as for example, the Ross's Goose. Others, like Bachman's Warbler, may occur in little pockets here and there over a wide area.

RESTRICTED WINTER RANGES OF RELICT SPECIES

Most of the species listed above have winter ranges that are as small as the nesting ranges, suggesting that they are at a competitive disadvantage at all seasons and in all places. Often, as with the Bristle-thighed Curlew, the Bachman's Warbler, and the Kirtland's Warbler, the winter range is insular. Species that winter on islands will have fewer resident species with which to compete, and these few will, on the whole, be less aggressive and competitive than ones native to continental areas. Resident insular birds live in a sequestered environment and in the course of time tend to become less adaptable than mainland species (see, for example, Bond, 1948: 221–226). The fact that some relict species reach their wintering grounds after what would seem to be unnecessarily long and hazardous migrations supports the hypothesis that insular winter ranges often do have definite advantages.

Most studies of the ecological relationships of sympatric birds give primary or exclusive attention to the breeding areas. If, however, the population of a species is drastically reduced in winter or on migration, the numbers reaching the breeding area may be so small that there is little competition for food, either intraspecific or interspecific. Even in resident species, winter rather than summer is often the crucial period, as is well known for many game species. Hence studies of interspecific competition among breeding migrant species must be analyzed with some caution (for further discussion of this and related problems see Gilbert, Reynoldson and Hobart, 1952).

Some years ago the late P. A. Taverner (1935) developed this concept on a broader basis. He pointed out that the tropical wintering area available to many species of North American migrants is much smaller than the nesting area, presumably resulting in severe competition in winter. This, he suggested, is the reason why more species of birds have become extinct in North America than in Eurasia, despite the longer history of persecution by man on the latter continent. The birds of Europe have a large wintering area available to them in Africa (Moreau, 1952), although many of them find it necessary to fly across the Sahara. Those breeding in Asia often migrate southwest into Africa too, but others winter in India, the East Indies, and even, in a few cases, in Australia.

Moreau (1952) has discussed competition between residents and migrants in winter, as did Mayr and Meise (1930) in their analysis of the theoretical aspects of avian migration.

It is possible, as Dr. E. Mayr has suggested to me, that the present reduced status of the Kirtland's Warbler and some other species with an insular wintering range is the result of an actual reduction in size of the islands on which they winter, caused by melting of the glaciers and rising sea levels. This may be a contributing factor in some cases, but the peculiar specialization that restricts the nesting habitat of this warbler to recent burns suggests that its limitations extend to the summer as well as to the winter range. Furthermore, several of the species listed above have a restricted winter range that is *not* insular.

THE "EVOLUTION" OF MIGRATION ROUTES

If, in declining or relict species, the winter range sometimes becomes, during the course of time, exclusively insular, we have a clue to the origin of certain rather baffling migrations such as that of the Bristle-thighed Curlew. This curlew is by no means the only shorebird that winters regularly in the islands of the central Pacific. The Golden Plover (*Pluvialis dominica*), the Tattler (*Heteroscelus incanus*), the Sanderling (*Crocethia alba*), and the Pacific Godwit (*Limosa lapponica*) also do. All of these, however, *except* the Curlew, also winter on the coasts of America, Asia, Australia, or Africa. It is natural to suggest that the Bristle-thighed Curlew is a relict species whose winter range *once* included such continental shores, but has *now* been restricted to the central Pacific islands, presumably because it could not compete successfully with shorebirds that winter in continental areas. As we have seen, the nature of its breeding range does make it seem likely that it is a relict species which once enjoyed a wider distribution.

In a somewhat parallel case, that of the Long-tailed Cuckoo (*Eudynamys taitensis*) which nests in New Zealand and winters on the numerous small islands of southern and central Polynesia (Bogert, 1937), there is no reason to believe that we are dealing with a relict species. It may be significant, however, that if this cuckoo were to winter in New Guinea or Australia, it might come into competition with the closely allied Koel (*Eudynamys scolopacea*), of which *taitensis* may be no more than an insular representative. Only in the Solomon Islands does *taitensis* winter in an area where *scolopacea* is resident, but the Solomons are outside the main winter range. Additional islands now submerged may have been present during the Pleistocene in the area between New Zealand and Polynesia and thus may have facilitated the evolution of this remarkable migration.

Thus, by assuming that migration routes and winter ranges may become constricted or altered by interspecific competition, we are able to explain how certain remarkable migrations to and from oceanic islands came into being. We need not fall back upon hypothetical land bridges or continental drift (Wolfson, 1948) as an explanation.

REMARKS ON EXTINCTION

Examination of distributional data will often provide a clue to the extinction or near extinction of certain species. The Labrador Duck is a case in point. Bent (1925) and others have correctly stated that the presumed small size of the breeding range of this duck made it especially vulnerable to persecution. As noted above, it seems to have been the only bird whose breeding range was restricted to the American coast of the North Atlantic. This leads one to suspect that it was already a relict species at the time it came to the attention of naturalists. Persecution by man led to speedy extinction.

In the Slender-billed Curlew one finds a species whose somewhat unusual migration and small wintering and breeding ranges suggest that we are again dealing with a relict species. If this is so, we are less surprised to learn from Stresemann and Grote (1943) that it has become greatly reduced in numbers. Study of distributional data may thus indicate that certain species are in special need of protection. Investigation of "natural" relicts may show us better how to conserve species like the Whooping Crane which have been reduced to relict status by the activities of man.

SUMMARY

When a species of bird of continental distribution is very restricted, ecologically or geographically (or both) in the absence of pronounced physical barriers, it is probably usually safe to assume that it is a

relict, that is, that the present distribution is less than it was in the past. Such relict species, when migratory, frequently have winter ranges that are as circumscribed as the breeding range itself. This suggests that the populations of such species may be, in some cases, more rigidly controlled by conditions on the wintering (or migratory) areas than by those encountered during the nesting season. This must be taken into account in assessing the importance of interspecific and intraspecific competition on the breeding grounds. Further, the winter ranges of relict species are often insular, presumably because competition is thereby reduced. Gradual restriction to an insular winter range as a species declines may, it is suggested, have produced certain remarkable migrations otherwise difficult to explain. Birds with a relict type of distribution will be especially susceptible to persecution or to man-made ecological changes and hence will require more than the ordinary degree of protection.

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