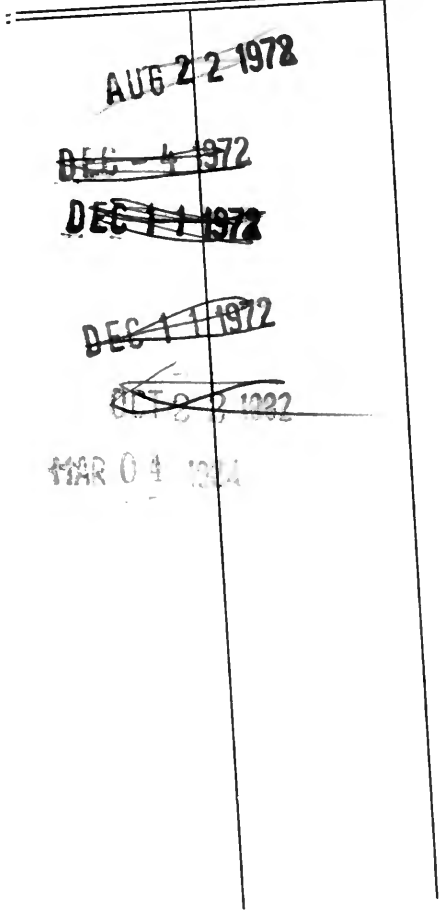

The Origin of the Land Birds of Tristan da Cunha

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Introduction

The remoteness and small size of the Tristan da Cunha Islands and the presence of five species of resident land birds, all of which belong to endemic genera (if we include the gallinule shared with near-by Gough Island), present one of the extreme cases of colonization of tiny, far-isolated oceanic islands by land birds. The surprisingly large number of stragglers that reach the islands is also noteworthy. The comparatively recent discovery of some of the endemic elements of this small avifauna (two of them in 1923) precluded their consideration by the classical zoogeographers of an earlier period. Wallace (1876, p. 271) considered the islands so little known he refused to discuss the relationships of their birds. He contented himself with pointing out that one sparrow described from Tristan da Cunha was said to have American affinities, while another was African. This last has proved to be an actual African species and the locality was found to be erroneous (see under *Serinus flaviventris*), but this single species, a large percentage of the small avifauna, apparently caused the islands to be considered commonly as part of the Ethiopian region. Newton (1893, p. 351) considered the avifauna to have as much affinity with South America as with Africa and included it in his Neotropical region (map facing page 311). W. L. Sclater, however, in his standard *Systema avium Aethiopicarum* (1924–30) included the Tristan da Cunha group in his African region, while Hellmayr, in his equally standard *Catalogue of the birds of the Americas* (Field Mus. Nat. Hist., Zool. Ser., **13**) does not include the birds of these islands. Hagen (1952), in his monograph on the birds of Tristan da Cunha, considers the endemic land birds to be the result of overseas colonization, partly from Africa, partly from America, and partly indeterminate.

The birds of the Tristan group have received considerable attention in recent years and have been the subject of several papers (see especially those of Hagen, 1952, and Elliott, 1953). However, certain points about the origin of the land avifauna needed further study, and when, through the generosity of Mr. Walther Buchen of Chicago, Chicago Natural History Museum received a small collection of birds from Tristan da Cunha, made by Mr. R. Upton in 1950–51, and from Colonel Hugh F. I. Elliott a few specimens from Gough Island, I took advantage of the opportunity to evaluate the relationships of the species and to consider the possible origin of the fauna.

The Islands

Location.—The Tristan da Cunha group of islands is one of the most remote areas in the world. It lies in approximately 37° S. Lat. and 12° W. Long. The nearest island is Gough Island, some 350 km. to the southeast. The Tristan group is about 2,400 km. south of St. Helena; 2,900 km. from Cape of Good Hope; 4,500 km. from Cape Horn; and 3,200 km. from the nearest part of South America, in Brazil.

Size.—This group, standing on the mid-Atlantic ridge, consists of three main islands: Tristan da Cunha, some 11 km. across and 2,329 meters high; and the smaller Inaccessible and Nightingale Islands, which lie within sight of the main island, about 32 km. to the southeast and about 19 km. from each other. Gough Island is about 13 km. long and reaches an altitude of 888 meters.

Habitat.—The islands are clothed with grass, brush, and ferns, and at least formerly there were trees that reached 25 feet in height. There seems abundant habitat for a variety of bird life. For descriptions and references see Murphy (1936, pp. 208 ff.), Munch (1945), and Hagen (1952).

Weather.—The prevailing winds would be expected to be an important factor in the colonization of the islands by birds. Southward from about 40° S. Lat. is the belt of prevailing westerly winds. In our area they blow from South America toward Africa. Munch (1945, p. 8) writes that Tristan da Cunha is situated in this "West Wind Belt," also called the "Variables," and that the prevailing winds are from the expected westerly direction, varying from northwest to southwest. The wind very often changes in the course of a day and seldom stays in the same direction for more than one or two days at a time. In summer, January to April or May, comparatively

light winds blow; in winter and spring, May to November, gales are frequent.

The Birds

The latest critical review of the avifauna by Hagen (1952) lists 35 species known from the Tristan group. Elliott's list (1953) adds 5 additional land birds, stragglers collected in 1950 and 1952, and hypothetical sight records of a few others. Most of the birds of the islands are pelagic species, with albatrosses and petrels well represented; skuas, gulls, and terns are a poor second, and penguins third.

The land birds known to occur and discussed below are listed here under the categories of residents and stragglers. The species whose occurrence is hypothetical (not based on specimens) and the erroneously recorded species are discussed later but are not listed here. No regular land bird migration comes near the islands. The number of land bird stragglers that have been recorded in a single year—5 species (6 individuals) in 1952—impresses one with the number of such stragglers that must occur each year.

RESIDENT SPECIES

Family Rallidae (Rails)

Atlantisia rogersi Lowe
Porphyriornis nesiotis nesiotis Sclater

Family Turdidae (Thrushes)

Nesocichla eremita eremita Gould
Nesocichla eremita procax Elliott
Nesocichla eremita gordoni Stenhouse

Family Fringillidae (Sparrows, etc.)

Nesospiza acunhae acunhae Cabanis
Nesospiza wilkinsi wilkinsi Lowe
Nesospiza acunhae questi Lowe
Nesospiza wilkinsi dunnei Hagen

STRAGGLERS

Family Ardeidae (Herons, etc.)

Egretta thula Molina

Family Rallidae (Rails)

Porphyrula martinica Linnaeus

Family Charadriidae

Zonibyx modestus Lichtenstein

Family Scolopacidae (Sandpipers, etc.)

Bartramia longicauda Bechstein
Erolia acuminata Horsfield
Actitis macularia Linnaeus

Family Hirundinidae (Swallows)

Hirundo rustica erythrogaster Boddaert

For comparison it is advisable to have a list of the land birds of the only other near-by island, Gough Island. This island, too, has an avifauna predominantly of sea birds, very similar to that of Tristan da Cunha though slightly poorer (Murphy, 1936, p. 213), and there are only two land birds recorded, one an endemic genus, the other an endemic subspecies of a Tristan-Gough endemic species and genus:

Family Rallidae (Rails)
Porphyriornis nesiotis comeri Allen

Family Fringillidae (Sparrows)
Rowettia goughensis Clarke

Discussion of the Species

In endeavoring to deduce origins I have first examined the resident birds for relationships shown by their morphology compared with that of their relatives elsewhere. Then I have considered the stragglers' mode of occurrence and place of origin, which might afford a clue to the relations of the resident birds.

RESIDENTS

Genus **Atlantisia.** Tristan Rail.

The genus *Atlantisia*, including but a single species, *Atlantisia rogersi* Lowe, is restricted to Inaccessible Island. Lowe (1928, pp. 99–130) studied the feather structure and anatomy of this bird and concluded that it was very distinct from other rails. He postulated a descent from non-flying ancestors of certain flightless rails, and, to account for distribution on islands, suggested dispersal on foot over former continental land masses such as "Lemuria" and Antipodea. Stresemann (1932) also examined the feather structure of this species, and concluded, probably correctly, that its flightlessness is a secondary regression from flying ancestors. For further discussion of feather structure see Sick (1937, pp. 261–263).

As an indication of its relationship, Peters (1934, pp. 166–168) placed it after the extinct *Nesolimnas* and *Cabalus* of the New Zealand area and before *Tricholimnas* of New Zealand and Lord Howe Island, genera which as a group are placed in the list after *Rallus* (wide-spread) and before *Oxtygonax* (South America).

The great modifications in skeleton and feathers indicate that this tiny flightless rail may be the oldest of the Tristan da Cunha endemics. From appearance and structure it seems impossible to suggest the stock from which it may have originated.

Specimens.—Chicago Natural History Museum has three skins, all from Inaccessible, of course: one collected by Rev. Philip Lindsay, September, 1928 (originally in spirits); one dated October, 1931, received from W. F. H. Rosenberg of London; and one, labeled a male, May 9, 1950, from Mr. R. Upton. They measure: wing, male 56, sex? 54, 55; culmen, male 24, sex? 23, 23; tarsus, male 23, sex? 23, 23 mm.

The specimen from spirits is brownish above, slaty below, and with conspicuous barring in the flanks, the plumage described by Lowe as the adult. The other two (1 male, 1 sex?) are generally blackish, with only a slight brownish tinge above; one is somewhat slaty below. This is the plumage Lowe considered immature.

Genus **Porphyriornis.** Tristan Coot.

This genus contains a single species, *P. nesiotis* Sclater, with one race (*P. nesiotis nesiotis*) confined to Tristan da Cunha and the other to Gough Island (*P. nesiotis comeri*).

P. L. Sclater (1861, p. 260) described the species as *Gallinula nesiotis* and considered it close to *G. chloropus* but of heavier build and shorter, less functional wings. Allen (1892) in describing the Gough Island race as *Porphyriornis comeri*, creating a new genus for it, said it was similar to the Tristan bird but differed especially in the greatly reduced amount of white on the edge of the wing and on the flanks. The new genus, he said, combined the coloration of *Gallinula*, the short thick bill and oval nostrils of *Ionornis* (=*Porphyrula*, part) and the stout feet of *Porphyrio*, with the added distinction of a greatly reduced wing.

Ripley (1954, p. 4) would merge this genus with *Gallinula* and derive the Tristan-Gough bird from a vagrant *Gallinula* from America.

I have not seen a specimen. From the description, if one considered color, bill, or feet alone as the best guide to relationships, one would consider *Gallinula* (in both Africa and America), *Porphyrula* (Africa and America), or *Porphyrio* (Old World) as ancestral. The relative size of the feet, in a flightless bird, seems a poor guide in attempting to relate it to flying ancestors. From characters, presumably *Porphyriornis* is derived from a *Gallinula* or *Porphyrula* ancestor, but precise allocation seems doubtful, and consequently the continent of origin is undeterminate.

Apparently little has been published about this species on Tristan. Peters (1934, p. 206) considered it extinct. Broekhuysen

and Macnae (1949, p. 98) even doubted its having existed and say only one specimen has ever been seen. However, P. L. Sclater (1861, pp. 260, 261) wrote of five living birds brought to Capetown, of which one reached London alive; at least two of the others as skins and one in spirit were in Sclater's hands then. Sharpe (1894, p. 167) lists two skins and part of a skeleton in the British Museum's collection. Mathews (1932, p. 19) records two specimens in the South Africa Museum, an adult and an immature, collected by Mr. P. C. Keytel (1907–1909).

A recently published record is an error, and Elliott (1953, p. 50) writes that the species is not remembered by any living person on the island and is undoubtedly extinct on Tristan. The species still survives on Gough Island.

Genus **Nesocichla.** Tristan Thrush.

This genus has but a single species, restricted to Tristan da Cunha where it occurs on all three islands. It has developed three subspecies.

Lowe (1923, pp. 523 ff.) has reviewed the history of its classification. It was treated as a thrush by Gould when he described it in 1855 but was placed in the Timaliidae in the *Catalogue of birds* despite a protest from Sharpe, who replaced it in the thrushes in the *Hand-list of birds.* Lowe was unable to allocate this heavy-billed, stout-footed thrush with somewhat rounded wing and tail to a definite place in the classification of the thrushes. He wrote that in view of the relationship between *Rowettia* and *Melanodera* a South American relation for this thrush might be expected. However, he was unable to relate it closely to any Middle or South American thrush, or to any African thrush. He discussed and dismissed the possibility of relation to *Zoothera* of the Himalayas. From external characters Lowe concluded that *Nesocichla* could be included in the genus *Turdus* with "reasonable justification"; the type of egg confirms this. Superficially it appears a true thrush modified by long residence on isolated islands. But on internal characters, notably the tongue, a long, gouge-shaped organ with a bifid tip and fringed extremity, and the much-reduced keel on the sternum, this Tristan thrush differed sharply from any *Turdus* known to Lowe, and amply merited generic separation in his opinion. Roberts (1948a, p. 62) related *Nesocichla* to *Psophocichla* (usually included in *Geocichla*) of Africa, but without comment.

Ripley (1952, p. 16), writing of the "true thrush" group in the Turdidae, says, "Two other primitive genera which seem related to *Turdus* are *Nesocichla*, the Tristan da Cunha thrush, and *Cichlherminia*, the forest thrush of the West Indies. Although by no means closely related to each other, I find them reminiscent enough in pattern and form to hazard a guess that the Tristan thrush came from some ancestral thrush stock of the New World, rather than Africa as has been suggested." He also says (p. 7) that the true thrushes of Old World origin have invaded the New World four times: the first invasion is represented by *Cichlherminia* (West Indies) and *Nesocichla* (Tristan da Cunha); the second by a *Hylocichla-Catharus* assemblage of widespread distribution; the third resulted in two *Zoothera*-like species in western North America and Mexico; and a fourth and final invasion populated the whole of both continents with a multitude of species of *Turdus*, rated as the most highly developed genus of true thrushes. In comparing *Nesocichla* with other thrushes I agree with Ripley (1952) that superficially they most recall *Cichlherminia* of the West Indies in being dark brownish thrushes with heavily marked breast, heavy bill, and long heavy legs. Two of the most obvious differences are the greater development of the rictal bristles and the presence of bare orbital skin areas in *Cichlherminia*.

However, as Lowe (1923, pp. 523–529) pointed out, *Nesocichla* also seems very close to *Turdus* itself. Bond (1950, p. 120), contrary to Ripley (1952, p. 7), considers that the coloration, habits, and nidification of *Cichlherminia* suggest relationships with the *Catharus-Hylocichla* group of thrushes. Dorst (1950) would unite *Hylocichla* with the genus *Turdus*. In view of this disagreement of recent students, it would seem that the subjective element is of considerable importance in their interpretation.

On the basis of external structure it seems advisable to consider *Nesocichla* as an offshoot of *Turdus*, specialized in isolation and with no very obvious affinities. Its specialization in internal structure (see Lowe, 1923, pp. 523–529) indicates a prolonged period of isolation. The greater development of *Turdus*-like thrushes in America and their scarcity in Africa might be taken as indicating an American origin.

Chicago Natural History Museum has the following specimens:

Nesocichla eremita eremita Gould

Tristan Island: 5 males, 3 females, all adults, June, September, October, 1950.

The measurements are as follows: Wing, male 100, 103, 105, 108, 109; female 103, 105, 106. Tail, male 82, 82, 84, 87, 87; female 80, 82, 85. Culmen, male 24, 25, 25, 26; female 25, 26, 26. Tarsus, male 35, 36, 37, 37, 37; female 36, 37, 37 mm.

Nesocichla eremita procax Elliott

Nightingale Island: 2 male subadults, 5 female adults, January, 1951.

The measurements of the adults are as follows: Wing 109, 109, 113, 115; tail 85, 85, 87; culmen 26, 28, 28, 29; tarsus 37, 37, 37, 38 mm.

Nesocichla eremita gordoni Stenhouse

Inaccessible Island; 1 male adult, 1 male subadult, March, 1951.

The measurements of the adult male are as follows: Wing 117, tail 89, culmen 27, tarsus 39.

The subadults are fully fledged and differ from the adults chiefly in having the more fluffy feathers of the under parts more distinctly spotted, with less tendency for the dark markings to run together into blotches or mottlings; in having considerable more or less concealed fulvous in the crown; and in having the fluffier feathers of the back with pale fulvous shaft streaks.

The series, from each island, are only moderately variable.

Though Lowe (1923) did not recognize subspecies when he worked out his Tristan collection, and W. L. Sclater (1930, p. 447) regarded *N. e. gordoni* as doubtfully distinct, and Broekhuysen and Macnae (1949, p. 105), with little material for examination, followed Lowe, our material shows this race to be very well-marked, as Mathews (1932) and Hagen (1952) have maintained.

Our specimen of *N. e. gordoni* of Inaccessible Island differs from our *N. e. eremita* in the slightly larger size; in the considerably duller, less bright fulvous of the ground color of the whole under parts; in the somewhat more extensive, darker, and more blackish markings of the under parts; in the darker upper parts; and in the brighter and more conspicuous fulvous outer edging of the primaries.

Our *N. e. procax* of Nightingale Island differs from our *N. e. eremita* as does *N. e. gordoni*. However, our series of female *procax* is very similar to our single adult male *gordoni*, and I cannot see the postulated larger size, pale gray tinge to the under parts, heavier spotting below, and primary coverts more uniformly tawny red (Elliott, 1954, p. 22) of *procax* in this scanty material.

Genus **Nesospiza.** Tristan Sparrows.

This genus contains but two species, both endemic on the Tristan da Cunha group of islands. The main points in the history of its classification follow. Cabanis in 1873 described *Nesospiza acunhae* as a new genus and species and could relate it to no African finch. He considered, on the basis of size, bill form, and foot structure with strongly developed toes, that it was near the South American genus *Melanodera*, but was separable by its more compressed bill and by its shorter, more rounded wing. Its loose feathers, short wing, and strongly developed toes he considered to indicate a life spent in thick brush and on the ground.

Lowe (1923, p. 521), in describing the second species, *N. wilkinsi*, pointed out that its larger bill with a curved culmen would doubtless be considered of generic importance by some systematists. However, Lowe pointed out that the occurrence of a large and a small form on the same island, in this group, recalls *Geospiza* and its many forms on the Galapagos Islands. He went on to say that generic separation of *wilkinsi* was inadvisable on the basis of both "practical utility" and "scientific justification." Besides implying that *acunhae* and *wilkinsi* were closely related he ventured no opinion of their relationships. Sushkin (1924, p. 38), presumably from his studies of the horny palate and perhaps other features but giving no details, wrote "*Nesospiza*, of Tristan d'Acunha, shows unquestionable affinities to the primitive American Emberizidae."

Lack (1947) considered that the two species of *Nesospiza* had South American affinities and were possibly related to *Rowettia* of Gough Island (see below).

Austin Roberts (1948a, p. 62) erected a new genus, *Crithagroides*, for *N. wilkinsi*, saying it was more closely related to the thick-billed seedeaters of Africa of the genus *Crithagra*. (The species Roberts [1948b, pp. 367–369] includes in *Crithagra* are included by W. L. Sclater [1930] partly in *Serinus*, partly in *Poliospiza*.) At the same time he pointed out that he considered *N. acunhae* to be more closely related to the siskins (*Spinus*) than to *N. wilkinsi*.

Mayr and Amadon (1951, p. 28) say the two species of *Nesospiza* seem to belong to the Fringillinae, perhaps near *Spinus* (rather than in the Emberizinae), but give no details. Hagen (1952, p. 229) considered them closely related to African *Spinus* or *Serinus*.

As to the relationship between the two sparrows and the advisability of using *Crithagroides* for the species *wilkinsi*, the differences that might be considered of generic value seem to apply

chiefly to the bill (figured by Lowe, 1923): much larger and deeper with a more curved culmen and the ridges on the sides from the upper part of the nostril forward giving a slight groove above it (a condition only suggested in *acunhae*). But in looking at the rest of the characters of the two species—the long dense plumage; the greenish, streaked color pattern; the general similarity in wing, tail and feet proportions shown by the averages (*wilkinsi*, wing 95.5, tail 79.7, tarsus 28; *acunhae*, wing 81.4, tail 72, tarsus 25); the short wing; and the squarish tail with rather slender pointed rectrices—their close relationship seems certain.

The finches of Tristan da Cunha have been considered as in an early stage of adaptive radiation that has been carried much farther in the finches of the Galapagos Islands and still farther in the honeycreepers of the Hawaiian Islands (Lack, 1947). Looking at these other groups, one finds that the range in bill characters in *Geospiza*, from *G. magnirostris* to *G. scandens* (figured by Lack, 1947, p. 19), and in *Psittirostra*, from *P. kono* to *P. psittacea* (figured by Amadon, 1950, pl. 10), or in *Loxops* (Amadon, 1950, pl. 9) is at least as great as the difference between the two finches from Tristan da Cunha, *acunhae* and *wilkinsi*. To be consistent it seems advisable to include both in one genus and consider *Crithagroides* a synonym of *Nesospiza*.

The Gough Island sparrow was described as *Nesospiza goughensis* (with immature buffy plumage described as *Nesospiza jessiae*) by Eagle Clarke and figured by him (see Clarke, 1905, pp. 255–257 and pl. 6). Lack (1947, p. 152) considers it as rather similar to *Nesospiza* in appearance but with a more elongate bill, and possibly to have evolved from *Nesospiza* stock. However, Lowe (1923, p. 512), in setting up the new genus *Rowettia* for it, pointed out that it was much closer to *Melanodera* of South America in the color pattern of both the adult and young (a similarity that Clarke had already noted, in part, when he described the species).

Mayr and Amadon (1951, p. 28) consider *Rowettia* not related to *Nesospiza* but derived from the South American genus *Melanodera* and hardly separable from it.

Chicago Natural History Museum has two specimens, an adult and an immature, of *Rowettia* from Gough Island, collected in February, 1952, by H. F. I. Elliott. The adult female measures wing 102, tail 78, culmen 21, tarsus 31 mm.

As Lowe pointed out, it is obviously close to *Melanodera* in color pattern but differs in elongated bill, the acuminate tail feathers

of the young plumage, the shape and color of the tail of the adult, and the relatively heavier feet and claws. The separation of *Rowettia* from *Melanodera* seems justified. As regards *Nesospiza, Rowettia* differs chiefly in the considerably more elongated bill and in color pattern, *Nesospiza* having in effect a more "primitive" pattern, more like the young of *Rowettia* but colored olive not buffy. The tail feathers of *Rowettia* are not so slender, but otherwise the details of tail, feet, wings, nostrils, and general proportions are very similar to those of *Nesospiza.*

In considering the relationships of *Nesospiza,* the external characters according to Cabanis pointed to *Melanodera.* But the color pattern is simpler, a greenish, generalized "sparrow" striping that recalls the *Spinus-Serinus-Poliospiza* relationship suggested by Austin Roberts, and Mayr and Amadon, and Hagen. Discussing external characters alone one might not come to a definite conclusion. Fortunately we have another character that seems to be of importance—the pattern of the horny palate, as pointed out by Sushkin (1924). In the *Spinus-Serinus-Poliospiza* group this has a main central ridge and two main lateral ridges, with a smaller, more slender pair of intermediate ridges that branch off from the main lateral pair and run parallel to the central ridge or converge toward its base. This is illustrated by the palates of *Serinus sulphuratus, Spinus spinus,* and *Poliospiza burtoni* (fig. 19, nos. 7–9) and is typical of many of the Fringillinae.

The situation is different in many of the emberizine finches of South America. In them there is a prominent pair of lateral ridges paralleling the side of the bill and a central ridge that forks toward its proximal end, often with a triangle or spur projecting forward between the arms of the fork (though this fork may be completely filled in, in some forms). This is illustrated by the palates of *Melanodera melanodera, Phrygilus patagonicus,* and *Sicalis olivascens* (fig. 19, nos. 1–3).

Though Sushkin's pioneer work has not been followed up in detail, I have personally examined a large number of the genera available and find these differences to hold for a large part of the groups Fringillinae (*Serinus,* etc.) and the Emberizinae (*Melanodera,* etc.).

Comparison of palates of the two species of *Nesospiza* discloses considerable differences (fig. 19, nos. 4, 5). The large-billed form has the posterior ends of the lateral ridges much enlarged and the arms of the fork of the central ridge much reduced. But the basic

similarity of the two patterns is plain. Their pattern is certainly that of the emberizine type, with a forked central ridge.

The horny palate pattern of *Rowettia* (fig. 19, no. 10) is also similar and of the emberizine type.

The possibility of relationship to *Emberiza* or *Fringillaria* of Africa seems remote, and a comparison with the palate of *Fringillaria tahapisi* (fig. 19, no. 6), of Africa, one of the most advanced emberizine types, shows the great amount of modification that has taken place in the basic pattern.

We may conclude that on general plumage characters a *Serinus* ancestor is perhaps indicated but that on foot structure, and especially on the structure of the horny palate, a relationship of *Nesospiza* and *Rowettia* with the Emberizinae of South America is apparently indicated. This latter alternative seems much the more conclusive.

One would assume that *Rowettia* was a younger species than *Nesospiza* and that both had been the result of separate colonization of their respective island groups by *Melanodera*-like ancestors that resulted in *Nesospiza* earlier, in *Rowettia* later.

Nesospiza wilkinsi Lowe

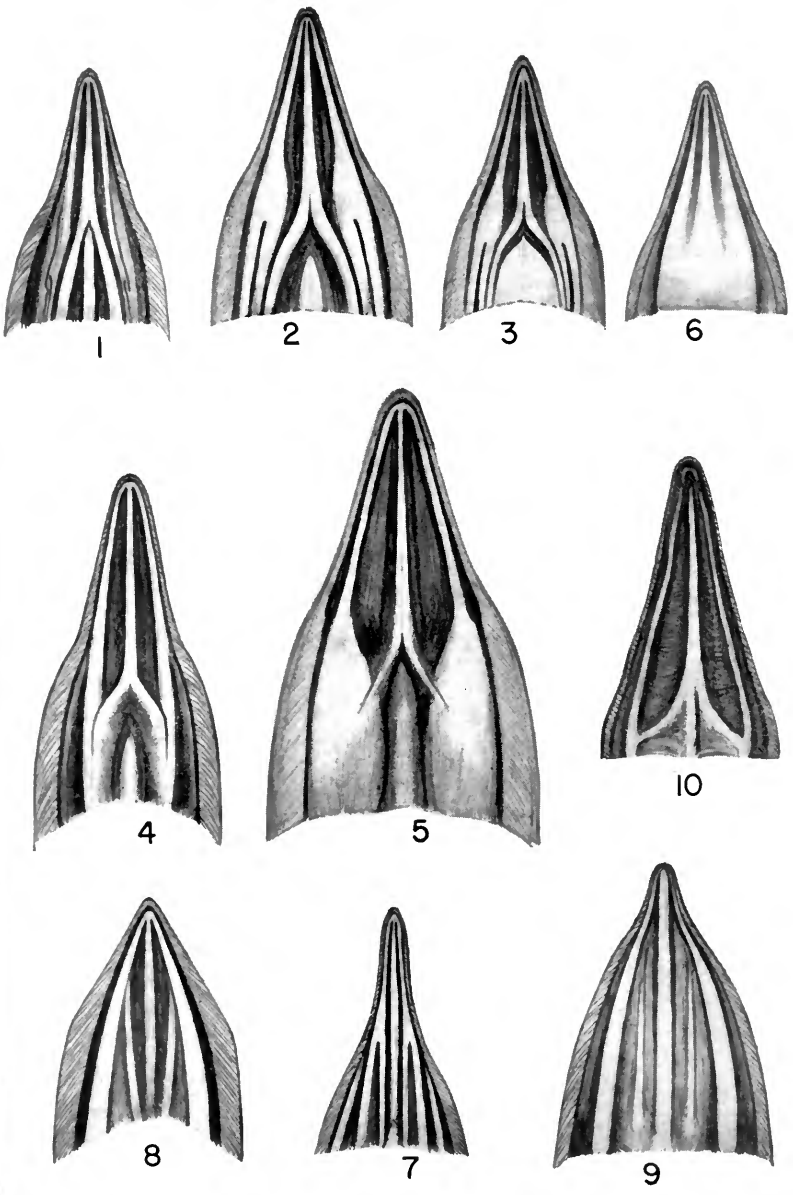
Material is insufficient to examine the geographical variation in the species for myself, so I briefly summarize Hagen's results (1952) with comments as to our Chicago Natural History Museum specimens. *N. wilkinsi* is known only from Nightingale and Inaccessible Islands. Hagen recognizes two subspecies:

Nesospiza wilkinsi wilkinsi Lowe. Nightingale Island.

Of this form we have four specimens. Two of these, a male and a female, compared with the other two are more greenish above and more greenish yellow below (less buffy yellow) with slightly bolder streaking and with grayish on the chin.

Wing, male 94, 94; female 95, 99 mm.

FIG. 19. The pattern of the horny palate of certain members of the Emberizinae (nos. 1–6, 10) and Fringillinae (nos. 7–9) drawn under a binocular microscope by Miss Margaret McKean and Miss Ruth Johnson. 1, *Sicalis olivascens* Lafresnaye and d'Orbigny (× 4); 2, *Phrygilus patagonicus* Lowe (× 4); 3, *Melanodera melanodera* Quoy and Gaimard (× 4); 4, *Nesospiza acunhae* Cabanis (× 4); 5, *Nesospiza wilkinsi* Lowe (× 4); 6, *Emberiza (Fringillaria) tahapisi* Smith (× 4.6); 7, *Spinus spinus* Linnaeus (× 3); 8, *Poliospiza burtoni* Gray (× 2.3); 9, *Serinus sulphuratus* Linnaeus (× 4); 10, *Rowettia goughensis* Clarke (× 4).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Nesospiza wilkinsi dunnei Hagen. Inaccessible Island.

This form was described on the basis of three specimens, 1 female adult and 2 immatures, as smaller than *N. w. wilkinsi:* Wing, female adult 89; immatures 87, 88.5 mm., compared with wing, male adult 94, 96.5; female adult 94.5, 94.5; immature 93.5. It appears to be a weak race, at best.

Nesospiza acunhae Cabanis

Nesospiza acunhae now occurs on Inaccessible and Nightingale Islands. Formerly it was found on Tristan da Cunha Island, where it has been extinct since before 1873 (Moseley, 1879, p. 122). Lack (1947, p. 152) writes that this species is divided into three subspecies differing in bill size, but only two subspecies seem to have been described. Hagen (1952, p. 160) recognizes only two races and points out that no series of Tristan da Cunha Island birds is extant, so that the question of a third race cannot be demonstrated. The two races, from Hagen, are:

Nesospiza acunhae acunhae Cabanis. Tristan da Cunha Island (formerly) and Inaccessible Island.

Of this race, Chicago Natural History Museum has three males and two females (wing, male 81, 81, 83; female 81, 83 mm.).

Nesospiza acunhae questi Lowe. Nightingale Island.

Characterized by Lowe as like *acunhae* but smaller (wing, male and female 76–81.5 against 83–88) and with smaller bill. Of Nightingale Island birds the Museum has two males and two females (wing, male 82, 83; female 79, 80 mm. While our material does not corroborate the postulated differences in size, Hagen's material did show it, and in addition he found the immature plumage to be more buffy in this race, so I accept it provisionally as a weakly distinguished race.

ACCIDENTALS

Egretta (Leucophoyx) thula Molina. Snowy Egret.

The normal range of this species is from the United States to Argentina and Chile.

There is one Tristan da Cunha record, a specimen, May, 1952 (Elliott, 1953, p. 49).

[**Egretta (Casmerodius) alba** subsp. Greater Egret.

The normal range of this species includes Africa (subsp. *E. a. melanorhynchos*) and South America (subsp. *E. a. egretta*). There is a sight record for Nightingale Island, April, 1950 (Elliott, 1953, p. 49), but the species should remain on the hypothetical list until a specimen has been secured.]

[**Bubulcus ibis** subsp.

The species' normal range is the Old World tropics and subtropics, with recently established colonies in northern South America that are thriving to such an extent that the species is colonizing North America. Perhaps it is also moving southward in South America.

Sight records for Tristan are given by Elliott (1953, p. 49). Its occurrence remains hypothetical, pending collection of specimens.]

[**Anatidae**

Sight records of a small flight of ducks, perhaps teal, add another item to the hypothetical list (Elliott, 1953, p. 49).]

Porphyrula (Ionornis) martinica Linnaeus. Purple Gallinule.

The normal range of this species is from the southern United States to Argentina and Peru. There are the following records for Tristan da Cunha:

Lowe (1924, p. 72): 1 immature received by British Museum.

Stenhouse (1924, p. 96): a second immature example (from Mathews, 1932, p. 48, who records Gordon's notes that it was the only one seen by his correspondent, Tom Rogers, in 1919).

Roberts (1948a, p. 61): 1 immature collected on Tristan da Cunha, April, 1945, and two others seen. The specimen is apparently moulting from immature into adult plumage.

Hagen (1951, p. 622): a regular visitor on Tristan da Cunha. The resident people have given a name to it, "gutter-snake," a name earlier recorded by Roberts.

Elliott (1953, p. 49): a regular, if presumably stray visitor, March to July, one record in November.

In addition to the above, Dr. Robert Storer of the University of Michigan Museum of Zoology tells me they have recently received two specimens, both immatures, a male and a female, from Tristan da Cunha, taken June 10 and 16, 1951, and Dr. Robert C. Murphy

writes me that the American Museum of Natural History, New York, has also received a specimen recently.

In Chicago Natural History Museum we have a specimen, immature, taken by Upton with data as follows: Tristan Island, May 5, 1951. Its plumage is completely immature and is very like that of American specimens.

Colonel H. F. I. Elliott writes in a letter of May 9, 1952, that two more *P. martinica*, a male and a female, were captured on Tristan, May 5, 1952. Possibly these are the two birds in Peabody Museum recorded by Ripley (1954, p. 5).

Almost surely the individuals of the species occurring in Tristan da Cunha represent strays from the Americas, amazing as it is. However, three individuals were recorded in 1951 and two in 1952. There is the possibility that a breeding colony has been established on the islands and these birds are the young of the year. If so, it would seem a very recent colonization from America. But either their regular occurrence as strays or their colonization helps us to realize how such "weak-flying" birds as rails have colonized so many remote islands.

Zonibyx modestus Lichtenstein. South American Dotterel.

The normal breeding range of this species is extreme southern South America (southern Patagonia, Tierra del Fuego, and the Falkland Islands. It winters north to Chile, Argentina and Uruguay. There is one Tristan da Cunha group record, a bird shot May 16, 1952 (Elliott, 1953, p. 50).

Bartramia longicauda Bechstein. Bartramian Sandpiper or Upland Plover.

Breeding range in North America; winter range on the pampas of South America. The one Tristan record is October 19, 1952 (Elliott, 1953, p. 50).

Actitis macularia Linnaeus. Spotted Sandpiper.

The normal range of this species is North America. It winters south to Peru, Bolivia, and Brazil. There is one Tristan record, February 5, 1952 (Elliott, 1953, p. 50).

Erolia acuminata Horsfield. Sharp-tailed Sandpiper.

The breeding range is in northeastern Siberia, with the normal wintering range from the eastern part of the Malay Archipelago

to New Zealand and the South Pacific Islands. There is one Tristan da Cunha record: June 16, 1950 (Elliott, 1953, p. 50). The route which this bird travelled to reach Tristan is problematic. Either east or west from its winter home in the eastern Malay Archipelago or the South Pacific is a long way, but perhaps the westerly winds make a route via South America seem the most likely.

Hirundo rustica erythrogaster Boddaert. Barn Swallow.

The normal breeding range of the American barn swallow is in North America and Mexico. It winters south to Argentina and Chile. As an accidental it has reached the Galapagos Islands, some 600 miles from Ecuador.

Hagen (1951, p. 622) records one specimen from Tristan taken on March 22, 1938, and Elliott (1953, p. 51) another on October 30, 1952.

SPECIES ERRONEOUSLY RECORDED

Serinus flaviventris Swainson

Loxia flaviventris Swainson, 1828, Zool. Jour., **3**: 348—South Africa.

Crithagra insularis Cabanis, 1873, Jour. Orn., **21**: 153—Tristan da Cunha.

Cabanis described *C. insularis* at the same time he described *Nesospiza acunhae*, both said to be from Tristan da Cunha, and commented on the one being pure African, the other of South American affinities.

Stresemann (1923) re-examined the type and considered it to represent a race of *Serinus flaviventris*. However, Mathews (1932, p. 47) writes that Dr. Stresemann tells him the locality was guessed and says *C. insularis* is a synonym of *S. flaviventris*.

The occurrence of an African species on Tristan da Cunha, to contrast with the known occurrence of South American species, would be very interesting. The validity of this locality is doubtful, and it seems inadvisable to admit the record.

Inter-Island Relationships

The three islands of the Tristan da Cunha group do not have all five endemic bird species occurring on each island. Though the group has one species in common with Gough Island, the other Gough Island bird belongs to an endemic genus. This is brought out by the following tabulation.

LOCAL DISTRIBUTION OF ENDEMIC LAND BIRDS

	Tristan da Cunha Island	Inaccessible Island	Nightingale Island	Gough Island
Atlantisia rogersi	0	1	0	0
Porphyriornis n. nesiotis[1]	1	0	0	0
Porphyriornis n. comeri	0	0	0	1
Nesocichla e. eremita	1	0	0	0
Nesocichla e. gordoni[2]	0	1	0	0
Nesocichla e. procax[3]	0	0	1	0
Rowettia goughensis	0	0	0	1
Nesospiza a. acunhae[4]	1	1	0	0
Nesospiza a. questi[3]	0	0	1	0
Nesospiza w. wilkinsi	0	0	1	0
Nesospiza w. dunnei[3]	0	1	0	0

1. Now extinct.
2. A well-marked race compared with *eremita*.
3. A weak race.
4. Now extinct on Tristan da Cunha.

It seems incredible that stock that colonized one of the Tristan da Cunha Islands over more than 3,000 kilometers of water from South America should not have covered the intervening 18 and 32 kilometers of water to the next islands. But only two of the five endemic species are recorded for all three islands: the small-billed sparrow (*N. acunhae*) and the thrush.

One wonders if the small-billed sparrow, said to have existed on Tristan da Cunha and extinct before 1873 (Moseley, 1879, p. 122) and not recorded there since, may not again colonize the island and give more definite data on inter-island colonization.

The two species that each occupy all three islands are divided into subspecies. The small-billed sparrow has one subspecies on Inaccessible and Tristan, and another (a weak race?) on Nightingale; the thrush has one subspecies on Tristan, a well-marked race on Inaccessible, and another weakly marked one on Nightingale. The thick-billed sparrow also occurs only on Nightingale and Inaccessible, with a race on each one.

The flightless gallinule occurred only on Tristan da Cunha Island (another subspecies on Gough), while the flightless rail occurs only on Inaccessible. Hagen (1952, p. 232) believes that ecological factors are responsible for this lack of uniform distribution.

However, this restriction of distribution may be an actual expression of difficulties of spreading from island to island; of the three species or subspecies occurring on two but not on three islands, two share the islands only 18 kilometers apart. The third shares

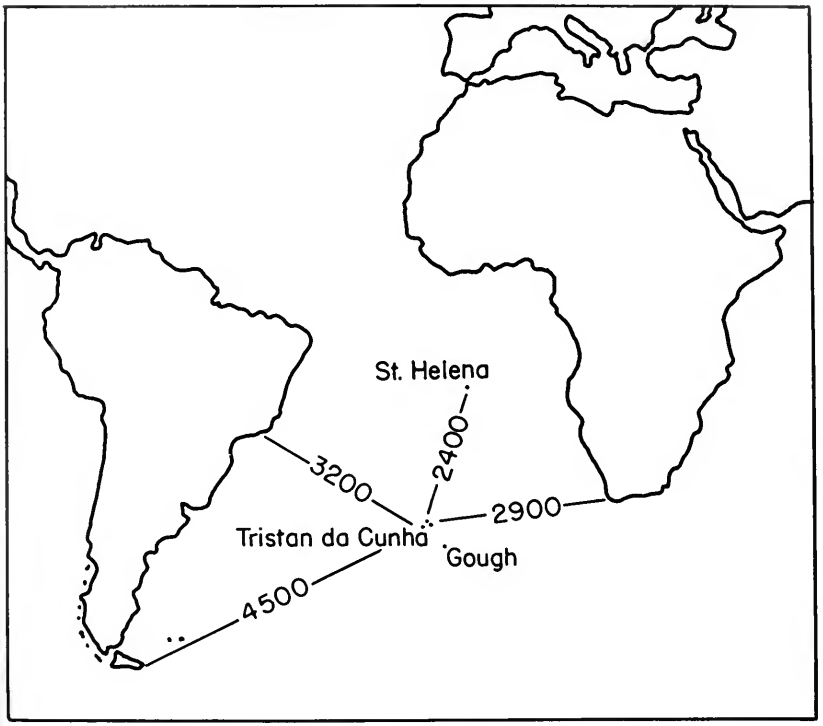

FIG. 20. Map showing position of Tristan da Cunha and Gough Islands in relation to Africa and South America. Distances in kilometers.

Tristan and Inaccessible, 32 kilometers apart. This apparent difficulty of dispersal may be a factor in providing isolation for the development of new species. Only one genus has produced species in the island, the sparrows (*Nesospiza*). This has been likened aptly to the condition on the Galapagos in miniature. Almost surely the thick-billed form evolved on one island, probably Inaccessible or Nightingale, from colonists of the small-billed form, after which it spread back to the other island, and the small-billed species spread to all three.

The endemic land birds of Gough Island number only two. Gough Island is about 350 kilometers farther southeast and this may be a factor, for land bird strays would be expected to be scarcer farther south, toward the Antarctic. Another factor may be the smaller size and altitude of Gough, only 13 kilometers in greatest length and 888 meters high, while the Tristan group, with islands in sight of each other, extends over more than 42 kilometers, and the

peak of Tristan reaches 2,329 meters in altitude. The latter is a considerably larger target, increasing the likelihood of strays hitting it, and visible from a greater distance to guide birds to it.

In view of the heterogeneous nature of the land birds, endemic and strays, recorded from the Tristan da Cunha group and Gough —a heron, a plover, three sandpipers, a rail, a gallinule, a swallow, a thrush, and three sparrows (two of a common origin)—indicating haphazard colonization, the relationship of the Gough Island birds to those of Tristan is surprising. The flightless gallinule of Gough Island is one subspecies; the other lived on Tristan's main island, apparently unable to colonize the other two! The Gough Island finch, *Rowettia*, appears to be a less specialized derivative (in color) of the same stock that produced *Nesospiza*. One is tempted to consider *Nesospiza* derived from *Rowettia*.

But the limited dispersal shown by the birds of the three Tristan da Cunha islands suggests that colonization to or from Gough Island would be improbable. The more southeastern position of Gough would require inter-island flights to cross the prevailing winds.

There is the possibility that certain species are more prone to be carried long distances than others, as with the purple gallinule at Tristan da Cunha in recent years and two records of barn swallows in 15 years. Perhaps the Gough Island flightless gallinule is not directly related to the Tristan form; each may be descended from different individuals of the same parent stock, some of which independently colonized each island. Their similar appearance is perhaps the result of similar change under similar severe ecological conditions. It seems improbable that the more specialized sparrows, *Nesospiza*, of Tristan are directly descended from the less specialized sparrow, *Rowettia*, of Gough, because of the position of the islands and the prevailing winds. Rather it might be that both of these, too, were evolved from independent colonizations of the common stock.

Discussion

The endemic land birds, the results of four colonizations, have evidently been on Tristan da Cunha a long time to develop their flightlessness (a rail and a gallinule), reduced sternum (thrush), and two species of an endemic genus (sparrows). The small rail, *Atlantisia*, might be considered to have had much the longest period in isolation on these islands; the flightless gallinule and the thrush,

both with flight mechanism modified, the next longest; the sparrows possibly came to the islands more recently. However, conclusions on the time necessary for their specializations are very tenuous.

The two Gough Island land birds more plainly represent a longer (gallinule) and a shorter (sparrow) period on the island.

The structure and color of the Tristan da Cunha birds provide scant evidence of relationship. *Atlantisia* is a small rail without obvious close relatives; the gallinule is apparently descended from a *Gallinula*- or a *Porphyrula*-like ancestor, living species of which occur in both Africa and America; the thrush seems to be derived from *Turdus*-like stock of a type more common in South America, but also occurring in Africa and Eurasia. The sparrows alone seem to indicate definite affinities with a group of South American sparrows.

In considering the collateral evidence from the two Gough Island endemics, the gallinule is only a subspecies of the Tristan da Cunha form; the sparrow seems definitely related to the same South American group of sparrows from which the Tristan da Cunha genus probably sprang.

Of the three Tristan da Cunha endemic genera and the one shared with Gough Island, only one can be definitely related to South American species; the others are indeterminate on characters. No African relationships emerge.

Of the two Gough Island genera, the endemic is definitely related to American sparrows; the other, the gallinule shared with Tristan da Cunha, is indeterminate.

The manner in which the ancestors of the Tristan da Cunha endemics might have arrived on the islands is discussed below.

(1) Land-bridges and lost continents: Percy Lowe (1928) seems to stand almost alone among modern scholars in considering that the Tristan da Cunha rail may have evolved from a section of the Rallidae that never had volant ancestors, and that it reached its present range on foot when Inaccessible Island was part of an ancient land mass, "Antipodea."

The evidence that some flightless rails did not include flying birds in their ancestry seems too slight to accept (Stresemann, 1932). To postulate an ancient land mass (or land bridge) to explain the distribution of a single species seems to involve mighty changes for a small result. The lack of, or the very slight corroborating evidence from, existing patterns of distribution of other species, the lack of patterns that would be expected if such postulated land

masses had been effective, and the existence of a simpler hypothesis that fits the known facts (see below) seem to justify discarding Lowe's idea.

(2) Continental drift: Wolfson (1948) holds that Africa and South America may have been adjacent and drifted apart at such a time that it affected the migration routes of present-day birds. If so, this continental drift could have had a profound effect on the avifauna of South America and Africa, and of the islands between. The same objections apply to this as to Lowe's theory of "Antipodea." For other objections to Wolfson's views see Amadon (1948) and Moreau (1949).

(3) Overseas colonization: This is generally accepted as the method of colonization by birds of such isolated island groups as the Galapagos and Hawaiian Islands (Lack, 1947; Mayr, 1943), and it is widely accepted as the way in which the Tristan da Cunha sparrow and thrush reached the islands from America.

AMERICAN RELATIONSHIPS

On Tristan da Cunha we know that five American bird species (unknown from Africa) of widely separated families (snowy egret, American dotterel, spotted sandpiper, Bartramian sandpiper, and barn swallow) have occurred at least once each. These individuals certainly came from the Americas. Another straggler, the purple gallinule, of the Americas, has been recorded a surprising number of times, and in one year three individuals were collected. These individuals almost surely came from the Americas. The possibility of overseas colonization is obvious. If it should be found that a breeding colony of purple gallinules exists on the islands it would still further strengthen the overseas colonization concept. Certainly the occurrences of the apparently weak-flying purple gallinule, a species that does not ordinarily travel in flocks, show that overseas stragglers from the Americas to Tristan da Cunha may be more than mere strays destined to perish in isolation, and demonstrate the probability of colonization.

To postulate that the flightless Tristan gallinule (with a race on Gough Island) evolved from such a colonization is reasonable.

Further, to postulate that the Tristan sparrows, showing South American relationships (and the Gough Island sparrow), evolved from ancestors that arrived in a similar manner is equally reasonable.

Though the thrush and the flightless rail are not clearly related to any American forms, they do not show closer relationships

elsewhere. It is logical to assume that their ancestors, too, arrived in the same manner.

African relationship absent.—Tristan da Cunha is slightly closer to Africa than to South America. In 1873, a South African finch was erroneously described as coming from Tristan da Cunha (see above). This presumably was the basis for the early zoogeographers' belief that the avifauna showed both African and American affinities. Elliott has recorded hearsay sight records of a predominantly Old World species, the cattle egret, that even if substantiated would not be conclusive evidence of colonization from Africa, as the egret has become established in South America and is colonizing North America. Otherwise there is no record of African land birds on Tristan da Cunha, and none of the endemics show close relationships with any African birds.

Prevailing winds a factor.—The reason for American colonization over a longer route, and the complete lack of it over the slightly shorter route from Africa (2,900 vs. 3,200 km.) appears to lie in the direction of the prevailing winds. These are westerly winds, Tristan da Cunha lying near the north edge of the belt of the "Great West Winds." These would help a bird from South America but hinder a stray flying from Africa.

It is interesting that the season of occurrence of the purple gallinule is mostly March-June, (one November record) and the barn swallow was taken also in March and in October. This is partly, at least, in the period of lighter winds, when storms and gales are less frequent. This may correlate in part with migratory movements in the Americas. It may also indicate that in the May or June to November period of strong gales and storms, stray land birds would be drenched, exhausted, and beaten into the sea.

Distance flown.—Recent physiological studies have attempted to prove that some species of birds can not fly distances as great as those that similar birds are known to have flown. Wolfson (1953) estimated on the basis of assumptions and speculations that the single flight range of a small passerine bird, the white-throated sparrow, is between 270 and 360 miles. Pearson (1950, p. 151) estimated that the ruby-throated hummingbird has a flight range of 385 miles (less than the 500 miles across the Gulf of Mexico that it is assumed to fly).

Actual open ocean distances covered by various small passerine birds as colonists and as strays are much greater. The Tristan da Cunha small passerine birds (or their ancestors) crossed at least

2,000 miles of ocean, and some of the ancestors of Hawaiian Island endemics had as far to go across the Pacific from America. The Galapagos Island endemic ancestors and the more recent stragglers to these islands have at least 600 miles of water to cross. A considerable number of North American birds have been found as stragglers in Europe, presumably having crossed the Atlantic; Norfolk Island *Zosterops* crossed 780 miles of water from Australia. These long flights were made over water. It is extremely improbable that the birds were able to rest on and certainly not to feed on the open Atlantic between South America and Tristan. The idea of natural "rafts" as aids is not very attractive.

The wind, of course, is an aid, probably an important if not an essential one in reaching Tristan. But even if a wind increased a small passerine bird's speed from say a normal 30 to a wind-aided 100 miles per hour, it would still take at least 20 hours on a direct course to reach Tristan.

Number of birds involved.—The Tristan group is less than 40 miles across. And yet in 1952 alone six species of "land" birds—a heron, a plover, two sandpipers, one gallinule (two individuals), and a swallow arrived there as strays over probably more than 2,000 miles of water. In 1951 three individuals of the gallinule were taken. One wonders if the gallinules have not established an undetected breeding colony there. But even if they have, we have five species (five individual birds in all) that arrived as strays in one year—seven individuals if we include the gallinules.

It is extremely improbable that all the vagrant wanderers that leave South America in a year set out in the precise direction of the 40-mile-wide Tristan group, and it is equally improbable that all the vagrants survive as far as the 2,000 mile mark. Rather, they probably set out in a random manner and the vast majority perish in the first few hundred miles. Imagination boggles at the concept of the total number of vagrants that must fan out each year.

Summary

Evidence indicates that the land avifauna of Tristan da Cunha is entirely of American origin and that the islands were colonized by accidental wanderers aided by the prevailing west winds.

The land birds of Gough Island are also undoubtedly the result of overseas colonization from South America. Despite their relationships with Tristan birds, difficulties of inter-island colonization and the position of Gough in relation to winds suggest that both

islands may have been colonized independently by similar, ancestral stock.

The great distances covered by these birds in overseas flight and the probably very large number of strays that set out and perish is mentioned.

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