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The Fauna of the Tristan Da Cunha Islands

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PART III. THE FAUNA OF THE TRISTAN DA CUNHA ISLANDS

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1. Introduction

Tristan da Cunha, Inaccessible, Nightingale and Gough Islands are similar in climate, physiography and vegetation, and form a single biogeographical province. Many animal species, including some endemics, occur on all of them, and the faunas of the four islands have the same general characteristics and show a common relationship to stocks in temperate South America. Any discussion of the fauna of the group must therefore consider all four main islands.

Such a general evaluation is rendered difficult by variations in the intensity of study of the different islands and of different taxonomic groups. It is probably true today that the native land fauna of the archipelago is adequately known in outline, and that no native vertebrate or abundant large terrestrial invertebrate species awaits discovery. However, the smaller and less conspicuous land invertebrates and the majority of the shallow-water marine organisms are undoubtedly underworked, and much remains to be discovered about the detailed distribution, ecology and interrelationships of the island faunas. The present paper is no more than an interim review of the extent and deficiency of current knowledge.

2. History of zoological exploration

Carmichael, in 1816, first collected animals on Tristan da Cunha (Carmichael 1818). A variety of scientific expeditions, including the *Challenger* expedition (Moseley 1879), the Scottish National Antarctic Expedition (Eagle Clarke 1905), the Shackleton-Rowett Expedition (Lowe 1923), the *Discovery* Committee's vessels, and the Norwegian Antarctic Expeditions (Christensen 1935) added to the list, as did several private investigators. But the first, and so far only, thorough zoological study of the three northern islands was made

Table 17. The history of zoological exploration in the Tristan–Gough group

number	expedition or collector	date of visit	islands studied	faunal groups studied	publication
1	British Garrison, Capt. D. Carmichael	1816	T	birds Mollusca Diptera Lepidoptera Coleoptera	Carmichael 1818 Gray 1824 Walker 1849 Walker 1857–62 undescribed
2	uncertain	1860–61	T	birds (*Porphyriornis n. nesiotis*)	Sclater 1861
3	H.M.S. *Challenger*	1873	T I N	birds Lepidoptera Coleoptera Myriapoda marine fauna	v. Willemöes-Suhn 1876 Moseley 1879 Waterhouse 1884 Pocock 1893 various *Challenger* reports
4	G. Comer (sealing expedition)	1888–89	G	birds (*Porphyriornis nesiotis comeri*)	Allen 1892 Verrill 1895
5	S.Y. *Scotia*	1904	G	birds, invertebrates	Eagle Clarke 1905
6	P. C. Keytel	1907–09	T	birds	Mathews 1932
7	Rev. H. M. Rogers	1922–23	T I N	birds (*Atlantisia rogersi*)	Lowe 1928 Mathews 1932
8	R.Y.S. *Quest*, H. P. Wilkins	1922	T I N G	birds Lepidoptera	Lowe 1923 Viette 1952
9	R.R.S. *Discovery*	1926	T	marine fauna	*Discovery* reports
10	R.R.S. *William Scoresby*	1927	G	marine fauna (some shore collecting)	*Discovery* reports
11	Rev. P. Lindsay	1928	T I N	birds	Rothschild 1928; Rand 1955
12	R.R.S. *Discovery*	1930	G	marine fauna	*Discovery* reports
13	R.R.S. *Discovery*	1933	T I	marine fauna	*Discovery* reports
14	M.S. *Thorshavn*, L. Christensen	1933	G	birds	Christensen 1935
15	Norwegian Scientific Expedition, Y. Hagen, E. Sivertsen	1937–38	T I N	all faunal groups	*Results of the Norwegian Scientific Expedition to Tristan da Cunha*
16	J. Kirby	1946	T I N	birds	Roberts 1948
17	Rev. M. Handley	1947	T I N	birds	Broeckhuysen & Macnae 1949
18	Lamberts Bay Canning Co. Expedition	1948	T I N G	birds, marine fauna	Broeckhuysen & Macnae 1949
19	A. N. and M. K. Rowan	1949	T I N	birds	Rowan 1951, 1952
20	R. Upton	1950–51	T I N	birds	Ripley 1954; Rand 1955
21	H. F. I. Elliott	1950–52	T I N G	birds invertebrates	Rand 1955 Elliott 1953, 1957, unpublished lists at Commonwealth Institute of Entomology
22	H. G. Stableford	1953–55	T I N	invertebrates	unpublished lists at Commonwealth Institute of Entomology
23	Gough Island Scientific Survey, 1956–56, M. W. Holdgate and M. K. Swales	1955–56	T G	all faunal groups	Heaney & Holdgate 1957; Holdgate 1958, 1960, 1961; Kuschel 1962; Swales 1965
24	South African Weather Station, J. J. van der Merwe	1956–57	G	birds, invertebrates	material in South African Museums Pacit 1959
25	Royal Society Expedition to Tristan da Cunha, D. E. Baird	1962	T I N	all faunal groups	Baird 1964

in 1937–38 by the Norwegian Scientific Expedition to Tristan da Cunha (Christophersen 1946). Later observations of the avifauna of the northern islands were made by Elliott (1953, 1957) and Rowan (1951, 1952). The only systematic study of Gough Island was made in 1955–56 by the Gough Island Scientific Survey (Heaney & Holdgate 1957). The areas worked by these expeditions, and by other contributors, are summarized in table 17 which is directly comparable with the analysis of botanical study forming table 1 in Wace & Dickson (1965, p. 275 above).

3. Composition of the fauna and reliability of the records

Appendix B (p. 394) is a check list, compiled from all the sources known to the present author, of the land and freshwatei fauna of the Tristan group. The marine fauna has been excluded because such a treatment presents greater difficulties in the present state of knowledge and because it lies rather beyond the scope of this paper. Table 18 summarizes the composition of the fauna and its known distribution among the islands, and also serves to demonstrate inequalities in research effort.

Table 18. Composition of the Tristan–Gough group land and freshwater fauna

taxonomic group	collector	Tristan		Inaccessible		Nightingale		Gough	
		endemic + native	doubtful + alien	endemic + native	doubtful + alien	endemic + native	doubtful + alien	endemic + native	doubtful + alien
REE-LIVING INVERTEBRATES									
Protista (from moss)	5	—	—	—	—	—	—	14	—
Rotifera (from moss)	5	—	—	—	—	—	—	4	—
Nematoda	5, 23	+	—	—	—	—	—	+	—
Platyhelminthes (fresh water)	23	—	—	—	—	—	—	1	—
Nemertea	15, 25	1	—	1	—	1	—	—	—
Annelida	22, 23, 25	—	6	—	—	—	—	2	5
Mollusca	1, 10, 15, 23, 25	5	3	1	—	—	—	7	3
Crustacea	3, 15, 23, 25	4	1	2	—	1	—	4	1
Myriapoda	3, 15, 23, 25	—	7	—	3	—	1	—	2
Insecta:									
Apterygota	23, 24, 25,	—	3	—	—	—	—	—	7
Orthoptera	15	1	—	—	—	—	—	—	3
Psocoptera	15, 23	—	2	—	1	—	—	—	3
Dictyoptera	25	—	1	—	—	—	—	—	—
Odonata	verbal, 25	—	1	—	—	—	—	—	—
Homoptera	22, 15, 23, 25	1	5	1	4	1	1	1	4
Heteroptera	15, 23, 25, 22	—	4	1	—	1	—	—	—
Thysanoptera	15	—	—	1	1	—	—	—	—
Lepidoptera	1, 3, 8, 15, 22, 23, 25, 21	9	6	4	2	4	—	4	3
Hymenoptera	15, 21, 22, 23, 25	—	1	—	—	—	—	—	2
Coleoptera	1, 3, 5, 15, 21, 22, 23, 25	6	14	13	4	9	2	6	4
Diptera	1, 3, 15, 21, 22, 23, 25	14	12	11	4	15	4	11	6
Arachnida:									
Acarina	15, 23, 25	3	—	—	—	—	—	2	—
Pseudoscorpionida	15, 23, 25	1	—	1	—	—	—	1	—
Araneida	5, 15, 23, 25	++	3	—	—	—	—	++	—
ARASITIC INVERTEBRATES									
Mallophaga	15	(17 species listed for group as a whole)							
Siphonaptera	15	(3 species listed for group as a whole)							
Hemiptera	15	(1 species, Tristan only)							
Diptera	15, 23	(1 species, Nightingale and Gough only)							
Acarina	15, 23	(3 species for group as a whole)							

	Tristan		Inaccessible		Nightingale		Gough	
ERTEBRATES	land	marine	land	marine	land	marine	land	marine
Aves: breeding, native	1	13	4	17	3	14	2	20
non-breeding, native	7	7	—	8	—	7	—	9
Mammalia: Pinnipedia, breeding, native	—	1	—	2	—	1?	—	2
Rodentia, feral, alien	3	—	—	—	—	—	1	—
Carnivora, feral, alien	1	—	—	—	—	—	—	—

The data in table 18 and Appendix B suffer from three major sources of uncertainty: undercollecting, incomplete taxonomic evaluation of collections, and doubt as to the true status of recorded species.

The smaller soil animals of the Tristan group are seriously underworked. The protistan and rotifer fauna of damp moss and soil is known only from a small sample extracted from a moss tuft collected on Gough Island in 1904 (Murray 1912; Penard 1912). Nematodes are certainly abundant in peaty litter and among damp ground vegetation but have totally escaped study, and the same holds for the tardigrades. Even the larger soil organisms—mites, Collembola and Annelida—have not been collected systematically or quantitatively. Lack of study of these groups in the Atlantic sector of the southern temperate zone is especially unfortunate at a time when detailed investigations of a comparable soil fauna are being made in Antarctic regions to the south (Gressitt 1964).

Even where collections exist, the study of the Tristan fauna, like that of many other areas has suffered from the present world shortage of specialists in many groups. Detailed study of the mites and Collembola obtained by the Norwegian Scientific Expedition of 1937–38 and the Gough Island Scientific Survey of 1955–56 has not yet been possible, while the Araneida, one of the commonest and most conspicuous elements in the invertebrate fauna of the group, are only now being examined. In many groups, furthermore, even were Tristan material to be examined in detail it would be hard to evaluate it properly in the absence of collections or critical taxonomic appraisals of material from temperate South America.

The status of the recorded species, tentatively suggested in appendix B and table 18, is also liable to considerable revision. Recent collecting has shown that *Delphacodes atlanticus* China 1958, described as endemic to the Tristan group, also occurs in Magellanic South America. *Geophilus tristanicum* (Attems) has been found in central Europe (Lawrence 1956) and *Ornithomyia remota* Walker in Argentina and Chile (Bequaert 1954). Lawrence (1956) suggested that three centipedes then known only from Tristan were probably alien species awaiting discovery in their homeland regions, and this supposition is confirmed by Blower (personal communication), who regards *Lithobius hageni* Lawrence as synonymous with *L. melanops* Newport, *Lamyctes tristani* Pocock as *L. fulvicornis* Meinhert and *Geophilus dacunhae* Lawrence, itself the same as *G. tristanicum* (Attems) as synonymous with *Necrophlocophagus longicornis*.

Re-examination of other genera and species has led similarly to their reclassification and an overall reduction in the number of listed endemics. Thus Kuschel (1962) showed that the two supposed endemic species of *Pentarthrum*, *P. carmichaeli* Waterhouse and *P. tristanensis* Brinck were the same, the former name having priority. Kuschel also argued that the Tribus Palaechtini (Curculionidae), established by Brinck (1948), which was the only endemic tribe claimed for the archipelago, is inseparable from the typically southern temperate tribe Listroderini, and that the five endemic genera within it could be combined without inconvenience. Hackman (1959) revised the drosophilid genus *Scaptomyza* Hardy, with the elimination of one Tristan endemic genus and three endemic subgenera. Current studies (Holdgate & Peake, in preparation) raise doubts as to the separation of the supposed endemic clausiliid mollusc genus *Tristania* Boettger from the European *Balea*, and the validity of the six species so far described within it (Odhner 1960). It is significant that these three groups—weevils, drosophilid flies, and clausiliid molluscs have in the past claimed the highest totals of Tristan endemic species, and are the only groups other than the land birds within which any marked degree of species radiation is apparent.

The birds, also, have lost endemic species and genera as a result of taxonomic revision. The two flightless gallinules from Tristan and Gough (the former now extinct) have latterly been treated as only subspecifically distinct while the genus *Porphyriornis* established for them may not be separable from *Gallinula* (Ripley 1954).

Further collecting and further study has thus shown that several species believed endemic to the Tristan group have a wider distribution, and has also resulted in a reduction of the number of recognized endemic species and genera and the elimination of the only supposed endemic higher category. These trends are likely to continue in future. The other uncertainty which arises over the status of species in appendix B concerns the native and alien elements. Seven aphids, two of which (*Neomyzus circumflexus* and *Aulacorthum solani*) were widespread in the undisturbed vegetation of Gough Island in 1955–56, fall into this category. Aphids are abundant in aerial plankton, but equally pests of cultivation and it is hard to assess their status on remote islands. The position of the small Hymenoptera which parasitize these aphids is similarly unclear. There are many other insects, including Collembola, and several enchytraeid worms, spiders, and mites, which could have reached the islands naturally but may in fact be imported, and an assessment of their position is likely to remain for the present a matter of rather sterile controversy.

4. General characteristics of the fauna

Despite the uncertainties and incompleteness of present knowledge, the Tristan fauna emerges as typical of that of an oceanic archipelago and certainly as well studied and as little disturbed by human activities as that of most comparably remote groups. Its salient features may be summarized as follows.

4·1. *Impoverishment and disharmony*

It is probable that the native fauna of the Tristan group lacks lumbricid worms, chilopods, diplopods, and slugs. Only one isopod is native and the land Mollusca are represented by only two genera with claims to native status (*Succinea* and *Tristania*). The former is well known as an insular colonizer (Gulick 1932; Quick 1957): the doubts surrounding the latter have already been mentioned. The only native terrestrial arachnid groups are the Pseudoscorpionida (with only one species, *Chelanops atlanticus* Beier), Acarina, and Araneida. Among the insects, Dermaptera, Dictyoptera, Plecoptera, Ephemeroptera, Trichoptera, Neuroptera and Mecoptera are lacking. Odonata have never been collected, and there is only one unconfirmed sight record (Baird, personal communication). Only one orthopteran and one thysanopteran are likely to be native and only two Hemiptera, *Nabis hageni* China and *Delphacodes atlanticus* China, come unquestionably into this category. Even the most abundant groups, the Lepidoptera, Coleoptera and Diptera, have a scanty representation and lack many families (such as Elateridae, Carabidae and Tenebrionidae) common in continental regions. In these general features the island group is typical of its class (Wallace 1902; Gulick 1932; Zimmermann 1948; Darlington 1957).

Table 19, which summarizes the total of species in each general category recorded from all the four islands and from the group as a whole, confirms not only the small total but the apparent gradation of fauna with area of the islands. Tristan, with a total of 69 endemic, native and doubtful species comes first; then Gough (64), Inaccessible (50) and Nightingale (39). It is tempting to compare these totals with those for the floras (in Part III) and see in them the effect of varying availability of habitat. Undercollecting on the two smaller islands, however, undoubtedly influences these figures and renders such a correlation unwise at the present time.

Tables 18 and 19 also emphasize that the Tristan group fauna appears unusually impoverished by comparison with many other oceanic islands. Twenty-six or twenty-seven Coleoptera with some claim to native status occur in the group, and there are thirty-two Diptera and ten established Lepidoptera in a total pterygote insect fauna of eighty-two species (excluding parasites). It is reasonable to estimate the total native insect fauna for the archipelago with a surface area of about 160 sq.km, at about 100. St Helena, the nearest Atlantic island, which has a smaller area (120 sq.km) has long been famous for its variety of endemic beetles, of which 128 were described before 1876 (Wallace 1902), and also has a number of remarkable Hemiptera and a total native insect fauna far out-numbering that of Tristan. Islas Juan Fernandez, in the Pacific, a group of similar extent

Table 19. Total terrestrial faunas of the Tristan–Gough Islands

		category					
island	total fauna	strict endemic	group endemic	native	doubtful	alien	breeding sea birds and seals
Tristan	141	4	22	28	15	58	14
Inaccessible	79	11	20	10	9	10	19
Nightingale	60	10	17	9	3	6	15
Gough*	105	10	14	18	22	19	22
all islands	239	35	29	40	39	71	24

* Protista and Rotifera omitted.

but somewhat warmer and nearer to the continent, has about 600 native insects, of which about 180 are beetles and 116 are endemic weevils (Skottsberg 1956). Most of the Pacific islands to have received study are far larger and also closer to continents and dispersal routes, but even so their faunas appear disproportionately rich by comparison with the Tristan islands. As Gressitt (1961) recognizes, similarly impoverished faunas typify the sub-Antarctic islands, such as the archipelago of Iles de Kerguelen, which has about seventy-three species of terrestrial arthropods including seventeen beetles and thirteen Diptera. This feature may be of significance in relation to the history of the insular fauna.

Impoverishment and disharmony are also marked among the marine littoral and sub-littoral fauna, though this is probably accentuated by undercollecting (Chamberlain, Holdgate & Wace, in preparation). Among missing groups are zone-forming cirripedes and mytilid molluscs. These are typical absentees from the smaller and more isolated southern islands (Knox 1960), as are shore crabs, and band-forming serpulid worms and ascidians. The causes of such impoverishment are discussed by Knox (1960).

4·2. *Endemism*

Seven terrestial genera (*Dimorphinoctua*, *Senilites*, '*Palaechtus*' sensu lato, *Atlantisia*, *Nesospiza*, *Nesocichla* and *Rowettia*) seem at present unchallenged as Tristan–Gough group endemics. Six more, *Tristania*, *Palaechtodes*, *Gunodes*, *Inaccodes*, *Tristanodes* and *Porphyriornis*, have been called in question. Even if all these thirteen were upheld it would be a small total for so isolated an archipelago. The number of endemic species—sixty-four only, on the best present estimate—is also small, and these are drawn from no fewer than thirty-seven genera. Thirty genera are represented only by single endemic species, two by two, two by three (*Dimorphinoctua* and *Hydrophorus*), one by a very dubious six (*Tristania*, itself perhaps inseparable from *Balea*), one by nine (*Scaptomyza* sensu lato), and one by eleven (*Tristanodes*, a member of the *Palaechtus* complex). About 60% of the total native terrestrial fauna is endemic, and less than 25% of the littoral and shallow-water marine benthic fauna, in which the endemism is also more uniformly spread by genera (cp. Holdgate 1960). While all estimates of endemism are approximate at present, it is suggested that the level may be lower than that in certain other oceanic island groups such as Hawaii, Juan Fernandez and St Helena.

A remarkable feature of the endemic element in the Tristan group is the wide distribution of many species over the four islands (table 19). This applies equally to terrestrial and marine species, and it is this wide-ranging habit which gives the fauna of the archipelago its highly unified features (Holdgate 1960). Only thirty-five out of the sixty-four supposed endemics are known from single islands (and this total may well be inflated by under-collecting). On Tristan, Nightingale and Inaccessible there are more than twice as many endemics shared with other islands as there are strict endemics. Tristan, although (as stated above) it has the *largest* total native, endemic, and 'doubtful' fauna, has fewer strict endemics (4) than any other island and hence is the *least* distinct of all the islands faunistically. Gough, with ten strict endemics and fourteen group endemics shows the clearest signs of faunistic isolation. These features may be correlated with the relative separation of the islands, Gough being much farther from the three northern islands than these are from one another. This may account for the relatively high level of strict endemism at Gough, and the very high proportion of shared endemics in the northern group. But the peculiarities of the Tristan island fauna suggest that another factor, age, is also involved. Tristan's few strict endemics suggest its youthfulness as a habitat, while the large size of its shared endemic element suggests recent population from the adjacent smaller islands by species previously differentiated in the archipelago and able to exploit the great variety of habitats which Tristan, because of its large area and great altitudinal range, can offer.

The endemics of the Tristan group have a further remarkable feature: flying capacity appears to be irrelevant as a factor influencing distribution between the islands of the group. Gough Island, the most isolated, shares fourteen endemic species and one endemic subspecies with the northern islands, and of these five can fly and ten cannot (table 20). In the endemic element of the whole archipelago the ratio of flying to flightless is 1:1·83. It is remarkable that primitive, highly distinct flightless endemic forms like the water-beetles *Senilites tristanicola* Brinck (1948) (Nightingale and Inaccessible) and *Bidessonotus involucer* Brinck (Inaccessible and Gough), and the strap-winged fly *Scaptomyza* (*Parascaptomyza*) *frustulifera* (Frey) (Tristan and Gough) should maintain identical populations on different islands. If these species have evolved to their present degree of distinctness in the Tristan group, one would be forced to conclude either that they have shown a remarkable degree of parallelism or that they have, despite the apparent improbability a considerable dispersal capacity.

It may be significant that the three species named above have their close relatives outside Tristan on other oceanic islands. *Scaptomyza* (*Parascaptomyza*) occurs on Tristan, Hawaii, the Azores and the Marquesas, with three cosmopolitan species while *Scaptomyza*

(*Trogloscaptomyza*) is known only from Tristan and Hawaii (Hackman 1959). *Senilites* is nearest to *Anisomeria* from Juan Fernandez and *Bidessonotus involucer* to a Juan Fernandez or Patagonian species (Brinck 1948). Viewing examples like these, it seems possible that part at least of the distinctness of certain Tristan endemics is due to their being 'relicts': that their parental mainland stocks have undergone more rapid evolution than the island populations or been replaced by later competitors. Such a persistence of primitive forms at the inaccessible periphery of their range is well known alike for vertebrates (Darlington 1957) and insects (Gressitt 1958) and, if the Tristan 'endemics' which are widely dispersed

TABLE 20. DISTRIBUTION OF ENDEMIC SPECIES WITHIN THE TRISTAN–GOUGH GROUP

endemic	flying ability	islands
Geonemertes nightingaleensis	nil	T I N
Tristanis tristensis	nil	T I G
T. ventricosa	nil	T G
T. costellata	nil	T G
T. costigera	nil	T G
Styloniscus australis	nil	T G
Nabis hageni	nil	I N
Dimorphinoctua pilifera	male only?	T I N
D. cunhaensis	nil	T I N
Protoleucania exoul	male only?	T I N
Bidessonotus involucer	nil	I G
Lancetes varius dacunhae	present	T I G
Senilites tristanicola	nil	I N
Pentarthrum carmichaeli	present	T I N G
Palaechtodes cossonides	nil	I N
Tristanodes scirpophilus	nil	T G
Limonia medi-atlantica	present	T G
Hydrophorus carmichaeli	present	T N
H. tristanensis	present	T I
H. christopherseni	present	T I N
Scaptomyza pectinifera	present	I N
S. altissima	present	T I N G
S. helvola	present	T I N
S. frustulifera	nil	T G
Dimecoenia tristanensis	present	T I N G
Chelanops atlanticus	nil	T I G
Porphyriornis nesiotis s.l.	nil	T G
Nesocichla eremita s.l.	present	T I N
Nesospiza acunhae	present	T I N
N. wilkinsi s.l.	present	I N

in the archipelago fall especially into the category of slowly evolving relicts, their similarity in different populations is more readily explicable. Further experimental and cytogenetic work on insular populations like these is evidently desirable.

Species radiation within endemic genera or subgenera in the Tristan group is most marked in four taxonomic groups, the weevils of the tribe Listroderini, clausiliid molluscs of the genus *Tristania*, drosophilid flies of the genus *Scaptomyza* and land birds of the genera *Nesocichla* and *Nesospiza*. These patterns, in their details of distribution, however, are not without anomalies. The listroderine weevils have fifteen species, all but two of which are confined to single islands, presenting at first sight an elegant example of geographical segregation of a species complex in an archipelago. Moreover, the genus *Tristanodes* may be divided (Brinck 1948) into four groups, regularly distributed on the three northern islands. Even in this detailed pattern, however, the unity of the northern faunas is apparent for, as Brinck remarks, most species are more closely related to a species of the same subdivision of the genus on another island than to species sharing their own island. The pattern suggests four wide-ranging 'group endemics', perhaps differentiated ecologically, which have further diverged into distinct stocks on each island. However, this regular and elegant pattern has one striking contradiction. Despite the apparent completeness of geographical segregation of stocks between the three northern islands, all only some 20 km apart, a single species, *Tristanodes scirpophilus* Brinck spans the extreme limits of the group to occur on the uplands both of Tristan and Gough.

Scaptomyza species show a more confused pattern of geographical segregation. Five endemic species are known only from single islands, two from two or more of the northern islands, one from all four islands and one only from Nightingale and Gough. *Tristania* is even more remarkable in that four out of the six described species occur both on Gough and in the northern islands, and on Gough Island, if five species are arranged in order of decreasing abundance: *T. tristensis*, *T. costellata*, *T. costigera*, *T. goughensis*, *T. flavida* and the areas from which each is recorded are mapped, it is found that each one has a distribution totally encompassing the known range of the next species. *T. tristensis* is universal from sea-level to the highest summits and occurs in all vegetation. *T. costellata* is a lowland species occurring especially in fern-bush, *T. costigera* is a form more exclusively of *Phylica* scrub, and *T. goughensis* and *T. flavida* have only been found with aberrant, unusually variable populations of *T. tristensis* and *T. costellata* in a tiny area near the east coast. Detailed analysis of the material (Holdgate & Peake, in preparation) suggests that these 'species' may in fact be little more than local forms or ecotypes.

Conversely, the land birds of the Tristan group show a clear-cut radiation pattern of classic type. The genera *Nesospiza* and *Nesocichla* are (or were) represented on all three northern islands, but not on Gough where the allied, monotypic genus *Rowettia*, probably ultimately derived from the same stock occurs instead. *Nesocichla* has different subspecies on each northern island, the Nightingale and Inaccessible races being closer together than either is to the Tristan population. *Nesospiza* has segregated into two distinct species, one (probably retaining the primitive condition) being a slender-billed generalized seed and insect eater (*Nesospiza acunhae*) and the other a thick-billed seed eater specialized for a diet in which the large, tough fruits of *Phylica arborea* feature prominently (*Nesospiza wilkinsi*). Little is known of the race of the former species which once inhabited Tristan, but both species are now represented by distinct subspecies on Nightingale and Inaccessible. As has long been recognized, this group of land birds thus shows a pattern paralleling in miniature that of the Galapagos finches. Equally, it is noteworthy that the differences between the island races are slight compared with the differences which all species show when compared with the nearest allied mainland forms and it is possible that some genetic mixing has continued between the several populations.

4·3. *Flightlessness in birds and insects*

It is well known that birds and insects of islands and mountains are commonly flightless (Darlington 1943), and this condition occurs in two out of the six native land birds and thirty-three out of the sixty-four native pterygote insects of the Tristan group (table 21).

The Diptera show the condition least, only four our of twenty-nine species being short-winged. Three of these are *Scaptomyza* (*Parascaptomyza*) species, and they are the only examples known in the genus despite its wide distribution on oceanic islands (Hackman 1959). The three flies form a series, *Scaptomyza* (*Parascaptomyza*) *angustipennis* being the least modified, *S.* (*P.*) *freyi* intermediate, and *S.* (*P.*) *frustulifera* the extreme case. The modification may have ecological significance in these species since all inhabit peaty ground tunnelled by nesting petrels: wings are of little evident use, and might be a positive hindrance to a fly which has adopted loose soil and litter as a habitat. The other flightless dipteran, the tipulid *Erioptera holdgatei*, is common on open uplands and in penguin colonies.

Table 21. Incidence of flightlessness in the Tristan–Gough native land fauna

group	apterous or brachypterous	some individuals or one sex brachypterous	fully winged
Aves	2	—	4
Orthoptera	1	—	—
Hemiptera	1	1	—
Thysanoptera	—	1	—
Lepidoptera	3	3	2
Coleoptera	19	—	4
Diptera	4	—	25
total	30	5	35

Six out of eight native Lepidoptera show some modification of the wings and three species of open uplands, *Dimorphinoctua cunhaensis*, *Dimorphinoctua goughensis*, and *Peridroma goughi* are strikingly brachypterous (Fletcher 1963). But the condition is most marked in Coleoptera, affecting nineteen out of twenty-three native species and being especially prominent in Curculionidae. This parallels the situation on many other islands, including St Helena (Wollaston 1877), Juan Fernandez (Skottsberg 1956), Kerguelen (Jeannel 1940) and Hawaii (Zimmermann 1948). In the birds, the two Tristan flightless species are both rails (*Atlantisia rogersi* and *Porphyriornis nesiotis*), and this situation also has parallels on many other islands. In discussing insular flightlessness it is important to emphasize that these inequalities between taxonomic groups in respect to their adoption of the condition exist. The classical Darwinian concept that natural selection promotes flightlessness on islands and mountains because it secures immunity from displacement by the prevailing high winds is, as Darlington (1943) points out, an over-simplification. Undoubtedly, such displacement is abnormally hazardous for insular or mountain species which have little chance of return to a satisfactory habitat once launched into the wind. Furthermore, the prevailing winds on such islands and mountains are generally stronger than average. However, other factors are also involved. The distances over which an insular species can profitably disperse are usually small, and this reduced need for dispersal capacity is accentuated by the greater uniformity of many insular habitats, the wide ecological amplitude (and hence wide occurrence) of many insular food plants (Wace & Holdgate 1958; Wace 1961), and the reduced interspecific competition to which the animals themselves are subject. These latter factors, operating in a negative way, must reduce the selection pressure favouring retention of flight capacity while the direct hazards of flight doubtless operate in addition. The degree to which species respond must vary according to their ecology and perhaps also to their inherent genetic variability: flying capacity is not likely to be equally liable to genetic variation in all taxonomic groups. The weevils and land rails of the Tristan–Gough group belong to taxonomic groups which appear to lose flying capacity rather readily even though, as Darlington (1943) emphasizes, they also have a way of life which must expose them rather little to prevailing winds. Their flightlessness perhaps arises more for negative than 'positive' reasons: if strong selection pressure does not promote its retention, there is a tendency for it to disappear. The upland Lepidoptera in the islands, and the apterous tipulid, on the other hand, certainly are exposed to winds when moving over the surface of the vegetation and their flightlessness may arise through direct selection. The Diptera have for the most part retained their flight capacity and this again probably reflects advantages gained from the condition which outweigh its perils. It is noteworthy that the only flightless Diptera in the group are soil dwellers, and hence have most probably adopted the condition through direct selection as a part of the process of invasion of an unusual new habitat.

4·4. *Marine birds, mammals, and invertebrates*

Oceanic islands generally lack native land mammals, and have rather few native land birds (with especially few raptorial species). Conversely, they are the breeding grounds of very large populations of sea-feeding birds and mammals. In the Southern Ocean this disproportion between land and sea ecosystems is accentuated by the richness of the marine plankton which supports huge populations of sea birds and seals, and by the scarcity of land suited to the breeding requirements of these species (Murphy 1964). This situation reaches its climax in the Antarctic, where vast bird and seal populations breed on the fringes of an unproductive cold desert. The Tristan–Gough group, on the other margin of the rich circum-Antarctic ocean, also has a large part of its surface utilized by breeding marine birds and mammals.

The mammals are represented by two seals, a fur seal, *Arctocephalus tropicalis tropicalis* (Gray) (King 1959 *a, b*) and the elephant seal, *Mirounga leonina* (L.). Some 13000 of the former species bred at Gough in 1955–56, and some hundreds at Inaccessible (Swales 1956; Holdgate 1958; Elliott 1953). The elephant seal population is smaller, probably only numbering a few hundred. The fluctuations in numbers of these species are intimately associated with human interference and are further discussed below.

A much larger number of sea birds breed in the group. Detailed lists are given by Elliott (1957) for the northern islands and a list for Gough Island prepared by M. K. Swales appears in Edinburgh (1961). Three species of albatross, one penguin and thirteen petrels breed at Gough (Swales 1965), and most of the same species occur in the northern islands, though the wandering albatross is less numerous there. The populations of burrowing petrels are extremely large. Rowan (1952) estimated that two million pairs of *Puffinus gravis* breed on Nightingale Island where almost all the available ground is honeycombed with their burrows. On Gough Island, *Pachyptila vittata*, *Pterodroma mollis*, *P. lugens*, *P. incerta*, *P. macroptera*, *Puffinus gravis*, *Puffinus assimilis*, *Pelecanoides urinatrix* and *Adamastor cinereus* are all very numerous and the ground is densely excavated (Swales 1965).

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The disturbance of the ground and heavy nitrogen deposition are important ecological factors (Wace 1961).

The invertebrate fauna of the islands also includes species of direct marine ancestry. Amphipods (*Orchestia scutigerula* and *O. platensis*) are abundant in the coastal zone and have been collected up to 75 m above sea-level on Gough Island. The freshwater fauna of Gough Island includes an isopod, *Iais pubescens* (Dana) and a planarian, *Procerodes ohlini* (Bergendal) elsewhere known only from the sea or brackish estuaries (Holdgate 1961). Such colonization of fresh water by marine forms, a common feature of oceanic islands, is presumably made possible by the lack of competition from specialized freshwater species just as the vast sea-bird populations are permitted by the absence of ground predators.

4·5. *Casual immigrants and stragglers*

Seven species of land bird (Rand 1955; Elliott 1957) and three Lepidoptera are recorded as casual stragglers to the Tristan–Gough group. Among the birds, the commonest vagrant is the gallinule *Porphyrula martinica*, which is so regular in its appearances at Tristan that it has acquired a vernacular name ('guttersnake'). Its occurrence is interesting in view of the presence of endemic gallinules on Gough and formerly on Tristan, and of the rail *Atlantisia* on Inaccessible. It is interesting to speculate on the chances of establishment of *Porphyrula* on Inaccessible or Nightingale, where there is no competing large gallinule and no ground predators. In this context, Elliott (1957) points out that all specimens examined by him were in an emaciated condition, and that establishment requires a quite unusual combination of factors.

Among the Lepidoptera, *Othreis apta* Walker has been taken on both Tristan and Gough and *Vanessa braziliensis* Moore and *Otosema odora* (L.) have been obtained on numerous occasions. *Vanessa braziliensis* may in fact be established, or may occasionally breed in the group, since one series of larvae from Tristan have tentatively been assigned to this species. A vanessid of uncertain species was seen on the island by D. E. Baird in 1962 (personal communication). Another vagrant insect reported from the group, a 'dragonfly' of unspecified type, was described to Mr Baird by a fisherman, also in 1962. There is nothing inherently improbable in such a sighting, since Odonata are among the groups known to be blown offshore from the South American coasts at certain seasons by westerly winds. Aboard R.R.S. *John Biscoe* in November 1961 the present author observed Aeschnid dragonflies in great numbers over the estuary of Rio de la Plata and numerous individuals came aboard the ship: one was still alive on arrival at Port Stanley, Falkland Islands, four days later, having been carried a distance about half as great as from South America to Tristan.

Dunnet (1964) has drawn attention to another unusual 'straggler' to the Tristan group. A specimen of the flea *Parapsyllus longicornis longicornis* Enderlein, recovered from a mollymawk, *Diomedea chlororhynchos* at Nightingale Island, is aberrant because this subspecies is characteristic of Ile St Paul while *P. longicornis dacunhae* is the form associated with Tristan birds.

Two important conclusions result from these records. First, it is clear that many animals can successfully reach oceanic islands like the Tristan group without establishing themselves. Almost all these records of vagrants are of large and conspicuous forms, but the chances of arrival of small, obscure species are as great or even greater: it is the smaller insects and mites which preponderate in aerial plankton. When it is remembered that the ten definite, or twelve probable, such stragglers to Tristan, amounting to about 10% of the total native fauna, have been observed in less than a century, it is easy to see how, over a period of some thousands of years such species which do not become established may outnumber the established fauna. Secondly, and as a corollary, some of the records of species from such islands which rest on single specimens or very short series could conceivably represent non-established vagrants and this chance must always be taken into account when analysing the faunas even of such very isolated land masses.

5. The origin of the Tristan–Gough fauna

5·1. *Relationships of the fauna*

All critical evaluations of the Tristan fauna in general (Holdgate 1960) or for particular component groups (Brinck 1948; Frey 1954; Kuschel 1962; Rand 1955) have emphasized its overwhelming affinity with stocks in temperate South America. Table 22 illustrates this for terrestrial and freshwater faunas. Of thirty-eight non-cosmopolitan native and endemic species or species-groups, nineteen occur in or have their nearest known relatives in South America, seven more in North and South America, two in North America only, three in South Africa, and four in the Palaearctic, while three groups of 'relict endemics' have their closest relatives in Hawaii, St Helena and other oceanic islands. Despite the relative proximity of St Helena (2100 km) and the Cape (3400 km) the small representation of their faunas in the Tristan group is especially noteworthy. In the marine fauna, the South American relationship is also strong, while there is a large southern temperate circumpolar element (Table 23) (Holdgate 1960; Chamberlain, Holdgate & Wace, in preparation). The detailed figures cited above and in table 22 may be somewhat affected by unequal collecting and non-uniform taxonomic study, but since the fauna of temperate South America is generally less well studied than that of South Africa it is likely that further work will strengthen, rather than weaken, the evidence for a South American relationship for the Tristan fauna.

5·2. *The age of the Tristan fauna*

The Tristan islands, judged by their erosional features, differ considerably in age. Tristan retains, especially in its upper levels, the simple conical form of a young volcano and no rocks older than 1 million years have so far been found there (Miller 1964). As Baker, Gass, Harris & Le Maitre (1964) point out, the island must have been characterized by intermittent activity, some of it on a considerable scale, throughout this period. Gough Island, second largest of the group, showed slight activity only 2300 years ago (Hafsten 1960*b*), but has a long and complex history (Le Maitre 1960) and rocks from its oldest exposed levels are 6 million years old. Inaccessible and the Nightingale group are more eroded, and the latter incorporates some rocks 18 million years old, although in both islands there is evidence of secondary eruptions extending into comparatively recent periods.

This geological information at least suggests that there is no reason for assuming land on the site of the present Tristan–Gough group earlier than the late, or at most the mid-Tertiary, and this may be taken as a maximal age of the flora and fauna. Furthermore, since the four islands are apparently of widely differing ages, there would be some reason to expect them to support faunas with differing degrees of endemism and with other signs of varying antiquity. In fact, as table 19 shows, despite their differing ages, the four islands have rather uniform faunas. This might suggest either a continuing interchange of species

TABLE 22. BIOGEOGRAPHICAL RELATIONSHIPS OF THE TRISTAN–GOUGH FAUNA

(Species marked with asterisks are naturally occurring casuals.)

species	supposed closest related species outside Tristan	biogeographical range
Tristania spp.	*Balea perversa*	Palaearctic
Delphacodes atlanticus	*D. atlanticus*	Magellanic South America
Nesothrips inaccessiblensis	*Bolothrips similis*	South Africa
Agonopterix goughi	*A. fulva*	North America
Udea hageni	*U. fulvalis*	Palaearctic
Nycterosea obstipata	*N. obstipata*	cosmopolitan
Peridroma porphyrea	*P. porphyrea*	cosmopolitan
**Otosema odora*	*O. odora*	Central America and northern South America
**Othreis apta*	*O. apta*	Central and South America
**Vanessa braziliensis*	*V. braziliensis*	South America
Bidessonotus involucer	*B. patagonicus* or *B. skottsbergi*?	South America and Juan Fernandez
Lancetes varius	*L. varius*	South America
Senilites tristanicola	*Anisomeria* spp.?	South America and Juan Fernandez
Ptinella natvigi	*P. matthewsiana*	St Helena
Leptacinus sp.nov.	?	South America or New Zealand
Coninomus sp.nov.	*C. heteronotus*	South America
Pentarthrum carmichaeli	*Pentarthrum* spp.	Chile
Palaechtus, *Palaechtodes*, *Gunodes*, *Inaccodes*, and *Tristanodes* spp.	*Listroderini*, especially *Hyperodes* and *Lixellus* spp.	South America
Erioptera holdgatei	*Erioptera* spp.	Palaearctic
Clunio africanus	*C. africanus*	South Africa
Telmatogeton sancti-pauli	*T. sancti-pauli*	South Africa, Ile Saint Paul
Hydrophorus carmichaeli	*H. poliogaster*	Chile
H. tristanensis	*H. elevatus*	Chile and Peru
H. christopherseni	preceding 2 spp.	Chile and Peru
Scaptomyza (*Trogloscaptomyza* species	*Scaptomyza* (*Trogloscaptomyza* spp.)	Hawaii
Scaptomyza (*Parascaptomyza*) species	*Scaptomyza* (*Parascaptomyza*) species	Hawaii, Marquesas, some cosmopolitan
Leptocera abdominseta	*L. abdominseta*	South America
Thoracochaeta seticosa	*T. seticosa*	North America
T. bracystoma	*T. brachystoma*	cosmopolitan except South Africa
T. zosterae	*T. zosterae*	cosmopolitan
Limosina plumulosa	*L. plumulosa*	cosmopolitan
L. heteroneura	*L. heteroneura*	cosmopolitan
Dimecoenia tristanensis	*D. caesia* or *D. densa*	South America
Ornithomyia remota	*O. remota*	South America
Chelanops atlanticus	*Chelanops* spp.	South America
Nesospiza species	Emberizinae spp.	South America
Rowettia goughensis	*Melanodera* sp.	South America
**Egretta thula*	*E. thula*	North and South America
**Porphyrula martinica*	*P. martinica*	North and South America
**Charadrius modestus*	*C. modestus*	South America
**Bartramia longicauda*	*B. longicauda*	North and South America
**Actitis macularia*	*A. macularia*	North and South America
**Tringa acuminata*	*T. acuminata*	Palaearctic and Australasia
**Hirundo rustica*	*H. rustica*	North and South America

between the islands, or that the present biota has been present in the archipelago for no longer than all four islands have been available as habitats (i.e. less than 1 million years). The truth is likely to lie between the two extreme viewpoints. Some faunal exchange between the islands is strongly suggested by the identity of endemic species on some or all of them. The low level of strict endemism on Tristan, the youngest island, on the other hand, suggests that its fauna may have been derived from the two nearby islands of Inaccessible and Nightingale and be therefore younger than theirs. The dating of such a colonization of Tristan is impossible: it cannot have occurred more than 1 million years ago, but may more plausibly be taken as having happened at the end of the major series of eruptions from the main Peak, in a much more recent period.

TABLE 23. ANALYSIS OF DISTRIBUTION OF GOUGH ISLAND MARINE INVERTEBRATES

(From Chamberlain, Holdgate & Wace, in preparation.)

	littoral species	sublittoral species
data available for	42	34
restricted to Gough	2	0
Gough and Tristan group only	8	3
total endemic element	10	3
non-endemic element	32	31
occurring in Tristan group	22	14
temperate South America	5	3
Magellanic region	14	12
Falkland Islands	11	9
South Georgia	5	4
Antarctica	2	3
South Africa	12	6
New Zealand	6	9
Kerguelen	5	6
St Paul and Ile Amsterdam	4	2
cosmopolitan	2	6

Considering the island group as a whole, the small size of the total native fauna, the low level of endemism, the paucity of endemic genera or higher taxonomic categories, the lack of species radiation, and the evidence that many primitive 'autochthonous' species (in the sense of Brinck (1948)) may be relicts owing their distinctness to evolutionary changes elsewhere, all suggest that the present fauna is a relatively youthful one. It is tentatively suggested that much or all of the Tristan group fauna has been established in the islands for a lesser period than the islands themselves have existed.

The Tristan archipelago today has a favourable climate with equable temperatures, monthly means at sea level ranging from 8 to 18 °C. Frost is rare at sea level and there is an abundant rainfall evenly spread by season. Ecologically, conditions are comparable with those in Chiloé or the Valdivian region of Chile, or parts South Island, New Zealand. The islands are substantially warmer than the Magellanic region of South America or any of the New Zealand shelf islands or the islands of the southern circumpolar belt. Yet, in its 'faunal spectrum', as Holdgate (1960) and Gressitt (1961) point out, the biota resembles that of the more southerly islands like Iles de Kerguelen: it is similarly impoverished, similar in the prevalence of Coleoptera (especially weevils), Diptera and Lepidoptera (especially Noctuidae) and in the lack of or paucity of Hemiptera or Orthoptera. Yet in terms of actual species-relationships (table 22) the affinities between the Tristan islands and these southern regions are slight. The similarity is a superficial one, and may reflect the exposure of all these islands to the same circumpolar winds and drift currents as dispersal agencies, and may indicate comparable faunal youth. Despite its present temperate régime, the Tristan group lies on the periphery of the sub-Antarctic region, within the range of drift ice, and at glacial maximum may have experienced cold or peri-glacial conditions near to those of the present sub-Antarctic belt. Any earlier Tertiary subtropical fauna would have been exposed to rigorous selection pressure by the cooling of the climate such as occurred generally in the late Tertiary in the southern hemisphere (Couper 1960), and these effects would reach their climax in the Pleistocene. At this period, there is reason to believe that the present sub-Antarctic islands, farther south, lost the greater part of their biota, and that present floras and faunas result largely from post-Glacial recolonization (Taylor 1955; Gressitt 1962; Skottsberg 1956). On a small island, climatic changes are somewhat buffered by oceanic influence (Hafsten 1960*a*, *b*), but the small area and limited range of habitats, and hence of refugia, prevent the long-distance movement of species such as may occur on a continent. Consequently, changing conditions may keep the biota in a state of flux and impoverishment. During the Quaternary period, Tristan's fauna may well have been affected by such fluctuations, while the prevailing influence of the west wind belt would develop and maintain affinities predominantly with the American and circumpolar rather than African region. Periodic volcanic phases might equally contribute to fauna instability, even though such activity has not prevented the development of a large and varied endemic fauna on Hawaii and other extremely active island groups.

Even though, as a generalization, one may suggest that the Tristan group fauna is young and had been largely gained during the Pleistocene period, this does not imply that all species on the islands arrived contemporaneously. Holdgate (1961) in discussing the freshwater aquatic fauna, established three tentative categories: ancient, intermediate and recent, defined largely by reference to the degree of taxonomic separation from related stocks outside the archipelago. Such a procedure is naturally approximate and takes no account of variations in rates of evolutionary change between taxonomic groups or species of different ecology. It is to be hoped that biometric studies of faunal remains in peat deposits and lignite beds on the islands will ultimately allow the rates of change of certain insular endemic stocks to be determined, and a reliable chronology established.

5·3. *Mode and conditions of immigration of the fauna*

There is no doubt that the Tristan da Cunha–Gough Island group of islands is wholly of volcanic origin (Baker, Gass, Harris & Le Maitre 1964; Le Maitre 1960). As already stated, there is no evidence for postulating land on the site of the present archipelago before the mid-Tertiary at earliest, while the late-Tertiary is a plausible date. Present discussions of continental drift theory suggest that the relative movement of the land masses was greatest before or during the Mesozoic, and that by at latest the mid-Tertiary present relative positions had almost been attained. While these chronologies are still indefinite, it seems at present plausible to assume that the Tristan islands attained their present floras and faunas under conditions of continental remoteness comparable with the present. On the other hand, the isolation need not always have been exactly as great as at present. Wilson (1963) has postulated that oceanic volcanic islands of this type arise on or near the crests of mid-oceanic ridges, and, as a consequence of convective upwelling and ocean-floor expansion, subsequently drift progressively toward the ridge flanks. If this has been the case, the Tristan group may, at the time of their origin, have lain a few hundred kilometres nearer to South America. Moreover, if Wilson's hypothesis is correct, certain sea-mounts like the Bromley plateau between Tristan and South America, the banks between Tristan and the Scotia Arc, and the prominent sea-mounts between Tristan and South Africa, may be the foundered remnants of more ancient volcanic islands. These could conceivably once have formed part of a rather discontinuous 'stepping stone' dispersal route, and this may encourage such authors as Christophersen (1939), Arnell (1958) and Brinck (1948) who feel that dispersal agencies must have been more effective at an earlier date than they are today. However, it must be pointed out that on Wilson's hypothesis these intermediate island groups should be far older than the Tristan islands and need not have coexisted with them.

The geological evidence seems, on the whole, to demand that the Tristan–Gough fauna be treated as one which has arisen by trans-oceanic dispersal under conditions relatively similar to those prevailing today, and if the arguments that the fauna is youthful are accepted, this is an evident necessity. Three traditional mechanisms for such trans-oceanic colonization are available for land organisms—direct aerial transport, transport attached to birds, and marine drift.

Holdgate (1960) pointed out the parallels between the composition of the Tristan–Gough fauna and that of catches of 'aerial plankton'. Table 24 carries this comparison somewhat further. Certain detailed similarities which the table does not bring out deserve special mention. Among the parasitic Hymenoptera sampled by Freeman (1945) the genus *Aphidius* was the most numerous, and the family Aphidiidae predominant: *Aphidius* is the commonest hymenopteran on Gough Island. Among the insects collected by Glick (1939) were Orthoptera of the genus *Tridactylus* (up to 1000 ft. altitude), and this is the sole genus of the group represented at Tristan. Other Tristan genera taken by Glick include *Nabis* (Hemiptera: Heteroptera) (to 1000 ft.), *Delphacodes* (Hemiptera: Homoptera) (common up to 5000 ft.), *Cercyon* (Coleoptera: Hydrophilidae) (to 1000 ft.), *Oxytelus*, *Atheta* and *Quedius* (Coleoptera: Staphylinidae), *Coninomus* (Coleoptera: Lathridiidae) (to 2000 ft.) and *Limonia* and *Erioptera* (Diptera: Tipulidae). With one additional genus of staphylinid, *Leptacinus*, these genera alone represent their families in the Tristan group. Glick's small sample of Lepidoptera is further of interest in containing forty noctuids and fifty-eight Microlepidoptera, the two groups most prominent on remote southern islands.

In general, the Tristan fauna agrees in its composition with the aerial plankton samples, in that no insect group recorded from Tristan is unrepresented in the air, while many of the groups most abundant in the air are also prominent on the island. But there are some anomalies. Collembola, mites and spiders are apparently over-represented on the island. Among the Coleoptera, Carabidae made up nearly 2% of Glick's total sample, yet are unrepresented at Tristan: conversely, weevils, which predominate on the island are never very abundant in the air (although generally present in significant quantities). Lepidoptera are relatively rarely taken in aircraft and other aerial traps yet are numerous on the islands. Clearly, while the available data suggest that many of the members of the Tristan land fauna could well have arrived as passive drifters in air currents, too elaborate an analysis of the data is unwise. There are also considerable differences between the different samples of aerial plankton in columns 1–3 of table 23, and these probably reflect differences in sampling method and region studied. Even greater extrapolations are involved in the comparison of these trapping results, over continents, from aircraft or captive balloons, with the expected natural rate of settling on an oceanic island. Current trapping over the

TABLE 24. COMPOSITION (%) OF THREE COLLECTIONS OF AERIAL PLANKTON COMPARED WITH THAT OF THE TRISTAN FAUNA

taxonomic group	(1) Hull, England Hardy & Milne (1938)	(2) Grimsby, England Freeman (1945, 1946)	(3) Tallulah, Louisiana, U.S.A. Glick (1939)	representation in the Tristan group fauna: (a) total	representation in the Tristan group fauna: (b) % of original immigrants
Collembola	—	under 0·2	0·1	7	8·6
Thysanura	—	—	0·1	1?	1·4?
Orthopera (s.l.)	—	—	under 0·1	1	1·4
Isoptera	—	—	under 0·1	—	—
Ephemeroptera	—	under 0·1	under 0·1	—	—
Psocoptera	0·2	10·2	0·3	3	4·3
Thysanoptera	2·4	2·7	0·4	1	1·4
Odonata	—	—	under 0·1	1?	1·4?
Hemiptera	35·7	27·5	21·5	8	10·1
Heteroptera	—	0·4	4·8	1	1·4
Homoptera: Aphididae	29·7	23·8	1·3	6	8·6
Jassidae	3·3	1·3	—	—	—
Psyllidae	1·9	0·9	2·3	—	—
Delphacidae	0·6	under 0·1	(Fulgoridae) (2·5)	1	1·4
Coleoptera	6·5	5·6	17·0	28	14
Staphylinidae	3·6	2·5	5·4	4	5·5
Lathridiidae	—	1·3	0·5	1	1·4
Chrysomelidae	2·9	0·8	1·9	—	—
Curculionidae	0·1	0·3	0·5	16	2·8
Hydrophilidae	0·1	0·2	0·1	2	2·8
Neuroptera	—	—	0·1	—	—
Trichoptera	—	—	under 0·01	—	—
Mecoptera	—	—	under 0·01	—	—
Lepidoptera	under 0·1	under 0·2	0·9	14	15·7
Diptera	31·3	37·2	43·5	33	32·9
Agromyzidae	0·8	1·2	under 0·1	—	—
Bibionidae	0·4	0·9	0·4	—	—
Borboridae	—	4·4	—	8	10
Cecidomyidae	0·8	3·1	0·2	—	—
Chironomidae	0·8	2·0	2·7	4?	5·6?
Chloropidae	5·4	7·5	8·5	—	—
Dolichopodiae	—	—	1·3	3	1·4
Drosophilidae	0·5	—	0·2	10	7·1
Ephydridae	2·9	1·6	2·8	3	2·8
Mycetophilidae	11·0	—	0·4	—	—
Phoridae	1·0	1·4	0·5	1	1·4
Psychodidae	0·1	—	under 0·1	(1 alien?)	(1·4)
Sciaridae	—	10·7	1·8	2	2·8
Tipulidae	0·1	—	1·1	2	2·8
Hymenoptera					
parasitic, total	16·5	16·6	7·1	3	4·3
non-parasitic	—	—	1·9	—	—
Araneida	0·1	0·5	1·1	numerous	numerous
Acarina	—	0·6	0·2	numerous	numerous

southern oceans and Antarctic by Gressitt and others (Gressitt, Leech, Leech, Sedlacek & Wise 1961; Yoshimoto & Gressitt 1959, 1960, 1961) should provide a more valid basis for such comparison.

The under-representation of Lepidoptera in aerial plankton catches may reflect sampling method, but certainly does not mean that these insects do not disperse widely over oceans. The presence of three species of straggler, almost certainly blown from South America to Tristan by the prevailing westerly winds, has already been mentioned. Hardy & Milne (1938) and Gislen (1948) cite records of Lepidoptera, Othoptera and other large strong-flying insects coming aboard ships at up to 500 km offshore, and the extreme instance of a swarm of locusts alighting on a vessel 2500 km out in the mid North Atlantic.

All in all, the correlation between the Tristan land arthropod fauna and the arthropod components of aerial plankton, or known long-range flying groups, is sufficiently close to support the proposal that air-borne immigration has contributed largely to the island fauna. The overwhelming American relationship of the fauna confirms this hypothesis, since the prevailing winds in the latitude of Tristan are from the west. Elliott (1957) and Rand (1955) have reached similar conclusions, while Gressitt (1962) has proposed that the youthful fauna of another southern Island, Macquarie Island, has arrived 'from the west, through air currents, sea currents or birds'. Airborne immigration is similarly favoured as a means of stocking Hawaii (Zimmermann 1948), Spitzbergen (Elton 1925), Samoa (Buxton 1935) and certain Indian ocean islands (Jouanin & Paulian 1954).

On the other hand, as Holdgate (1960) pointed out, oligochaetes, Mollusca and some larger wingless arthropods are not taken in aerial plankton and must have arrived by some other means. Transport attached to birds has been favoured for such groups: Gislen (1948) cites a record of fresh mollusc spawn on the feet of a duck shot over the Sahara and Falla (1960) points out that a significant percentage of young, burrow-nesting, oceanic petrels fly with down patches in their neck regions.

Such down can readily become contaminated with debris from the nest tunnel and may act as a vehicle for dispersal: in the Tristan group this mechanism may account for the wide dispersal of flightless, soil-dwelling invertebrates over the four islands of the group. Birds may also transport freshwater and marine organisms, and Hartmann (1964) has referred to the remarkable occurrence, in Finland, of a parthenogenetic population of the South African copepod *Cyprilla humilis*, presumably transported by migrating Arctic terns.

The dispersal patterns of the birds of the Tristan group cover much of the world and offer potential transport from a great variety of places. Some species, including giant petrel (*Macronectes giganteus*), wandering albatross (*Diomedea exulans*) and cape pigeon (*Daption capensis*) make circumpolar migrations in the westerly winds. Others, notably the yellow nosed albatross (*Diomedea chlororhynchos*) have been shown to move from Tristan especially to the South African coast and may perhaps mingle or rarely interchange with other members of the species which form the breeding group in Ile St Paul and Nouvelle Amsterdam. Such an interchange best explains the anomalous occurrence of a flea typical of the albatrosses of Amsterdam at Nightingale (Dunnet 1964), and may have some bearing on the presence at Tristan of the chironomid fly, *Telmatogeton sancti-pauli*, named from Saint-Paul, and the common occurrence on the two island groups of several plants. Until recent human disturbance, the avifauna of both archipelagos had much in common. Yet other birds, notably the greater shearwater (*Puffinus gravis*) migrate annually in the North Atlantic, where they are common off the North American and European coasts. Within the Tristan–Gough group themselves birds probably move not infrequently from island to island, and this may be especially true of non-breeding, predatory, skuas (*Catharacta skua hamiltoni*) of which at least one, marked on Gough, has been recorded as moving north to Nightingale (Swales 1965).

There is, perhaps, less reason to postulate marine drift as a mechanism of colonization of the Tristan group by land animals. However, driftwood, seeds and pumice are known to be carried long distances in the circumpolar current of the West Wind Drift, and the possibility that shallow-water marine species may be transported attached to such debris, or to detached masses of kelp, is considerable (Knox 1960; Marr 1963). Marine species may also have colonized the deeper waters around the island along the submarine ridges linking the group with the Antarctic, and Marr (1963) shows this to be plausible for certain unstalked crinoids.

There seems no reason to conclude that the present, available natural dispersal mechanisms are insufficient to explain the nature and relationships of the depauperate, youthful fauna of the Tristan–Gough island group. Further, more critical study may perhaps reveal anomalies which test these hypotheses more strictly and compel some greater elaboration. Until then, economy of hypothesis surely demands that the observed distributions be explained, as far as possible, in terms of the observable mechanisms.

6. The native ecosystem

6·1. *Freshwater fauna*

Holdgate (1961) has described the freshwater fauna of Gough Island and at the same time commented on the scanty available information about that of the three northern islands. The habitats on the several islands are rather dissimilar. On Gough the upland plateaux are peat-covered and the blanket bog covering is broken by a number of small pools. From the upland mires, permanent torrential streams cascade into the valleys along the north and east coasts, or more abruptly down the western gulches and cliffs. The largest stream on Gough Island, that in The Glen, is some 5 m wide and has numerous deep pools: in flood the stream may be up to $1\frac{1}{2}$ m deep while even in drought it maintains a steady flow of water. Other streams only slightly smaller drain the principal valleys. In contrast on Tristan, while there are some deep, permanent small lakes in secondary volcanic craters, and some semi-permanent rivulets draining montane bogs, most of the main watercourses (in the gulches) run only after heavy rains. The drainage at other times percolates underground, welling up at the shore, but in one place providing a constant stream across the Settlement Plain. Nightingale is also a relatively waterless island (apart from the swamp pools known as the Ponds) while Inaccessible is rather intermediate, and, like Gough, has some permanent streams. Sea spray, blown over the islands, probably accounts for the high sodium and chloride concentration recorded in Gough Island fresh water and is undoubtedly a factor of general ecological significance.

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On Gough Island, six out of a total of eight aquatic species were collected in the richest station on the Glen stream. A minor lowland stream sampled, and an upland stream, were both poorer faunistically. The most widespread phytophagous animal is the larva of the ephydrid fly *Dimecoenia tristanensis*, whose hooked prolegs are adapted to maintain a grip on alga-covered submerged stones on which the animals browse. A dytiscid, *Lancetes varius dacunhae* is the most widespread freshwater animal, occurring in some places where no other freshwater species have been collected, and it is thought to subsist in considerable part on terrestrial animals accidentally falling into the water. A second dytiscid, the much smaller, weaker, *Bidessonotus involucer*, is restricted to weed-choked runnels and is cryptic in habit. On Inaccessible and Nightingale the third dytiscid in the group, *Senilites tristanicola*, inhabits pools. In contrast to these three fairly widespread carnivores and one very widespread phytophagous species, the other species collected occurred only in the lowland reaches of the Glen. Two were of direct marine ancestry; an isopod, *Iais pubescencs* and a planarian, *Procerodes ohlini*. In the Glen stream also, an oligochaete, *Lumbricullus* sp., a conspicuous bright red colour in life, was found amid gravel. It, like the isopod, may have been a detritus feeder, and their restricted range may in part be correlated with a lack of sediments in these generally torrential habitats.

The salient feature of the aquatic fauna of Gough Island appears to be its poverty and the apparent slightness of the interdependence between the component species, which give the impression that each, arriving at a different time, has expanded to the limit of the available range without being much affected by the others. Further study may well prove, however, that this is purely a superficial impression.

6·2. *General features of the terrestrial fauna of Gough Island*

Table 25 lists the main components of the fauna of Gough Island, which is the only member of the group on which collections have been made deliberately in relation to the vegetation types. The only difference between the units used and those defined by Wace (1961) and Wace & Dickson (1965; this Report, Part II) are:

(*a*) The designation of a category of 'coastal mixed vegetation'. This was an association of *Carex* spp., *Scirpus* spp., *Apium australe*, *Cotula goughensis*, *Rumex obtusifolius* and various grasses, including *Poa flabellata*, which grew just above storm line on parts of the east coast near the Glen.

(*b*) The designation of a category of 'mixed grass-sedge' within the fern-bush. This was used in the field to refer to a number of communities of disturbed ground, including grass and sedge turf (often dominated by *Holcus lanatus*) along stream banks, and certain early seral stages (often dominated by *Scirpus* spp.) in the recolonization of peat slips.

(*c*) The omission of peat mires as an upland category. In the field certain streamside samples, on peat mires, were treated as a form of grass and sedge wet heath communities while the very species-poor mire expanses were insufficiently studied to merit the inclusion of lists.

Table 25 suggests that the fauna as a whole shows some measure of impoverishment with altitude, although the richer fauna of the lowland fern-bush may well reflect its greater complexity as a habitat and its more luxuriant vegetation as compared with the thin, wind-eroded plant mats of the uplands rather than indicate any direct influence of altitude on the animals. From the table certain 'lowland' and 'upland' species and groups do, however, become apparent:

LOWLAND SPECIES OR GROUPS		
Porcellio scaber	abundant below 180 m	absent above 300 m
Orchestia scutigerula	maritime	absent above 75 m
Cylindroiulus latestriatus	abundant below 180 m	absent above 180 m
Ectopsocus briggsi	abundant in fern-bush	absent above 180 m
Aulacorthum solani	frequent near coast	absent above 120 m
Neomyzus circumflexus	frequent in fern-bush	absent above 460 m
Coninomus sp.nov.	abundant in fern-bush	absent above 180 m
Tristanomyia frustulifera	common in fern-bush	absent above 180 m
Aphidius cp. *sonchi*	occasional in fern-bush	absent above 180 m
Oxychilus alliarius	frequent below 100 m	absent above 300 m
Tristania costellata	abundant in fern-bush	absent above 300 m
UPLAND SPECIES OR GROUPS		
soil Lumbricidae and large Enchytraeidae	inconspicuous below 300 m	abundant and evident above 450 m
Tristanodes scirpophilus	not below 300 m	widespread 300–780 m
Peridroma goughi	rare below 300 m	widespread 300–780 m
Dimorphinoctua goughensis	rare below 300 m	widespread 300–780 m

The remainder of the fauna is divisible into a category of more or less ubiquitous species (*Styloniscus australis*, *Delphacodes atlanticus*, *Chelanops atlanticus*, *Succinea flexilis*, *Tristania tristensis*) and a final category of species either too rare or too unevenly collected to be assigned to any group.

Swales (1965) points out that a similar zonation of breeding distribution exists among the birds of Gough Island, and this probably also holds, to a lesser degree for those of the other islands as well (Hagen 1952; Elliott 1957). The three albatross species breed as follows:

Diomedea exulans dabbenena: open uplands, in wet heath and montane moor above about 500 m, on Gough and Inaccessible.

Diomedea chlororhynchos: in fern-bush, and occasionally in tussock grassland, below about 500 m on Gough, below about 900 m on Tristan.

Phoebetria fusca: on cliff ledges at all elevations on Gough, and in steep coastal tussock. Among the smaller petrels some, including *Pterodroma mollis*, *P. brevirostris*, *Pachyptila vittata*, *Puffinus assimilis elegans*, and *Pelecanoides urinatrix* are especially abundant in the fern-bush zone, below about 500 m. *Puffinus gravis* is especially a bird of coastal tussock grassland and the single penguin species, *Eudyptes crestatus* breeds almost exclusively in this vegetation type. Burrowing petrels are less numerous on the uplands, but some, including *Adamastor cinereus* are typical of the higher levels. The land birds also show preference for certain zones and plant formations. On Gough Island, the gallinule *Porphyriornis nesiotis comeri* is commonest in fern-bush and some areas of tussock, while the 'bunting', *Rowettia goughensis*, occurs at all levels but is commonly observed in the open on the uplands and along the beaches.

TABLE 25. DISTRIBUTION BY HABITAT OF THE GOUGH ISLAND FAUNA

	vegetation type										
				fern-bush			wet heath		montane moor, etc.		
	coastal fringe mixed	tussock grassland	tussock grassland (penguin rookery)	*Histiopteris* fern-brake	mixed grass sedge	*Phylica arborea* + *Blechnum palmiforme*	*Blechnum* + *Empetrum* heath	grass + sedge heath	*Rhacomitrium Empetrum*	*Agrostis carmichaeli*	rocks, etc.
ıber stations...	6	3	2	9	5	10	2	5	2	3	2
ıdes (m)	4–8	30–75	15	10–120	10–100	45–180	300–460	450–780	600–830	450–900	660–675
nchytraeid sp.	—	—	—	—	1	1	4	2	2	1	1
nchytraeus sp.	—	—	—	—	—	—	2	1	2	5	2
'enlea sp.	—	—	—	—	—	1	—	—	—	3	—
redericia sp.	—	—	—	—	—	—	—	1	—	—	—
umbricid sp.	—	—	—	—	—	—	—	1	4	1	2
ıccinea flexilis	—	1	2	1	2	—	2	5	2	4	2
xychilus alliarius	1	1	—	2	1	1	2	—	—	—	—
'ristania tristensis	—	4	2	1	4	3	4	5	—	—	4
'. costellata	—	—	—	3	1	4	2	—	—	—	—
'. costigera	—	—	—	—	1	1	—	—	—	—	—
'. goughensis	—	—	—	1	—	—	—	—	—	—	—
'. flavida	—	—	—	1	—	—	—	—	—	—	—
ɔrcellio scaber	3	4	5	4	3	4	2	—	—	—	—
yloniscus australis	1	1	—	2	1	2	4	5	2	5	4
rchestia scutigerula	1	3	—	—	—	—	—	—	—	—	—
ylindroiulus latestriatus	3	3	2	5	3	5	—	—	—	—	—
ypogastrura sp.	—	—	—	4	—	—	2	—	—	—	—
otoma sp.	—	—	—	4	—	—	—	—	—	—	—
legalothora sp.	—	—	—	2	—	—	—	—	—	—	—
ninthinurus sp.	—	—	—	4	—	—	—	—	—	—	—
ɔlsomia sp.	—	—	4	—	1	—	2	—	—	—	—
roisotoma sp.	—	—	4	—	—	—	—	—	—	—	—
ɛrobasis annulata	—	—	—	—	—	1	—	—	—	—	—
ctopsocus briggsi	—	—	—	2	—	3	—	—	—	—	—
'elphacodes atlanticus	2	4	—	3	3	1	4	3	—	—	—
ılacorthum solani	3	—	—	2	—	—	—	—	—	—	—
'eomyzus circumflexus	—	—	—	2	1	2	2	—	—	—	—
'hopalosiphum padi	3	—	—	—	2	—	—	—	—	—	—
ıcksonia papillata	—	—	—	—	—	—	2	—	—	—	—
uedius mesomelinus	—	—	—	1	—	—	—	1	—	—	1
ɛptacinus sp.nov.	—	1	—	1	—	—	2	—	—	—	—
ɔninomus sp.nov.	1	—	—	5	—	3	—	—	—	—	—
ɛntarthrum carmichaeli	—	1	—	—	—	—	—	—	—	—	—
isc. Coleopt. larvae	1	—	—	1	1	1	4	1	—	—	—
'ristanodes scirpophilus	—	—	—	—	—	—	4	3	—	—	—
imorphinoctua goughensis	—	1	—	—	—	—	2	1	—	—	—
ɛridroma goughi	—	—	—	—	—	—	2	—	—	3	—
octuid larvae	1	1	—	—	1	1	2	1	2	3	4
'lonopis crocicapitella	1	—	—	—	—	—	—	—	—	—	—
ristanomyia frustulifera	1	—	1	4	—	2	—	—	—	—	—
imecoenia tristanensis	1	—	4	1	—	—	—	—	—	—	—
ırascaptomyza altissima	1	1	—	—	—	1	2	—	—	—	—
'egaselia sp.	1	—	2	—	—	—	—	—	—	—	—
'mosina plumulosa	1	—	—	—	—	—	—	—	—	—	—
ıcellia maritima	1	—	—	—	—	—	—	—	—	—	—
horacochaeta zosterae	1	—	—	—	—	—	—	—	—	—	—
rnithomyia remota	—	—	—	—	—	—	2	—	—	—	—
ɛlmatogeton sancti-panti	—	—	—	1	—	—	—	—	—	—	—
ychoda severini	1	—	1	1	—	3	—	—	—	—	—
'ioptera holdgatei	—	—	4	—	—	—	—	—	2	—	2
'monia medi-atlantica	1	—	—	—	—	—	—	—	2	—	—
ıittia sp.	1	—	1	1	—	2	—	—	—	—	—
'adysia sp.	—	—	1	—	—	1	—	—	—	—	—
ɔlichopodid larvae	—	—	1	—	—	—	2	1	—	3	2
her dipt. larvae	—	1	5	—	1	—	—	1	2	1	2
ɔhidius cp. *sonchi*	3	—	—	1	1	1	—	—	—	—	—
ɛdioptera cp. *subaptera*	1	—	—	—	—	—	—	—	—	—	—
ıelanops atlanticus	—	4	—	1	—	—	2	1	—	—	—
'aneida spp.	3	4	2	5	3	5	4	4	—	3	4
ıarina various spp.	1	—	4	3	—	2	4	—	—	—	—
red predatory sp.	—	—	—	1	—	2	4	2	—	—	2
ticks, spp.	—	1	—	1	—	1	—	1	—	—	—
	27	16	16	31	19	24	26	19	9	12	13

The figures in each column indicate frequency:

5, present in over 80 % of samples.
4, present in over 60–80 % of samples.
3, present in over 40–60 % of samples.
2, present in over 20–40 % of samples.
1, present in over 0–20 % of samples.

6·21. *Fauna of fern-bush*

Fern-bush was the most complex vegetation type and habitat examined on Gough Island, showing both vertical layering and horizontal subdivision into a mosaic of component communities. The broad distribution of the fauna within it is shown in table 26. This fauna can be subdivided, from an ecological viewpoint, into several categories.

TABLE 26. DISTRIBUTION OF SPECIES WITHIN FERN-BUSH VEGETATION

Phylica branches		*Histiopteris* and *Dryopteris* understory		*Blechnum palmiforme*		*Histiopteris* fern-brake	
Araneida	va	Araneida	va	Araneida	va	*Coninomus* sp.	va
Tristania tristensis	f	*Chironomid* sp.	f	*Ectopsocus briggsi*	a	Araneida	a
T. costellata	f	*Tristania costellata*	f	*Tristania costellata*	f	*Tristania costellata*	a
T. costigera	o	*T. tristensis*	o	*T. tristensis*	f	*T. tristensis*	f
Smittia sp.	f	*Delphacodes atlanticus*	o	*Porcellio scaber*	o	*Neomyzus circumflexus*	f
Ectopsocus briggsi	o	*Tristanomyia frustulifera*	o	*Styloniscus australis*	o	*Aulacorthum solani*	f
(red mite)	o	*Neomyzus circumflexus*	o	(red mite)	o	*Delphacodes atlanticus*	f
Psychoda severini	o	*Ectopsocus briggsi*	o	*Neomyzus circumflexus*	r	*Tristanomyia frustulifera*	o
Bradysia sp.	o	*Psychoda severini*	o	*Coninomus* sp.	r	*Styloniscus australis*	o
noctuid larva	vr	*Coninomus* sp.	o	Lepidoptera larva	r	*Porcellio scaber*	o
		Aphidius sonchi	o	*Psychoda severini*	r	(red mite)	r
		(red mite)	r			*Tristania goughensis*	r
		Styloniscus australis	r			*T. flavida*	o
		Porcellio scaber	r			*Aphidius sonchi*	r
						Ectopsocus briggsi	r

soil and litter

Cylindroiulus latestriatus	va	*Megalothora* sp.	f
Porcellio scaber	a	*Sminthinurus* sp.	f
Styloniscus australis	a	*Tristania tristensis*	o
Araneida	a	*T. costellata*	o
Acarina	a	enchytraeid spp.	o
Oxychilus alliarius	a	*Chelanops atlanticus*	r
Isotoma sp.	f	*Tristanomyia frustulifera*	r
Hypogastrura sp.	f		

Frequency symbols: v, very; a, abundant; f, frequent; o, occasional; r, rare.

(*a*) *Phytophagous species*

Phylica itself is almost immune from attack by invertebrates. Its small, hirsute, leathery leaves show virtually no signs of damage, and the only common invertebrates on the branches, the small clausiliid molluscs of the genus *Tristania*, probably feed on lichens and algae coating the boughs. This is probably also true for the small psocids *Ectopsocus briggsi* and *Cerobasis annulata*. *Tristania* species and *Ectopsocus briggsi* occur widely also on the tree ferns and *Histiopteris* and *Dryopteris* of the field layer and on pure stands of *Blechnum palmiforme* and *Histiopteris incisa* outside the *Phylica* thickets. Their food here is uncertain.

Within the *Histiopteris* fern-brake the number of phytophagous species is greater and several of them show more precise associations with plants. The lathridiid *Coninomus* sp. is very abundant on *Histiopteris* itself: the aphids *Neomyzus circumflexus* and *Aulacorthum solani* occur chiefly on *Apium australe*, and the delphacid, *Delphacodes atlanticus* on *Scirpus* spp. and grasses.

(*b*) *Soil and litter species*

Oligochaetes are inconspicuous in the litter and deep uncompacted peats of the fern-bush, though small enchytraeids are probably far commoner than the limited sampling suggests, and nematodes are undoubtedly abundant. Collembola and mites are similarly abundant but under-collected, but the most conspicuous elements in the fauna are the introduced diplopod *Cylindroiulus latestriatus*, the introduced isopod *Porcellio scaber*, and the native isopod *Styloniscus australis*. Among the molluscs, *Tristania* species are not characteristic of litter and hardly occur at all in the soil, but the introduced *Oxychilus alliarius* is abundant. No insect larvae were found tunnelling dead or fallen wood. As soon as fungal breakdown is advanced, millipedes, isopods, mites and other soil animals become numerous in the interstices and these undoubtedly accelerate breakdown. This lack of specialist log-borers, and also the predominance of supposedly alien species in the soil fauna may lead to speculation about the initial processes of litter breakdown before these species arrived. It is conceivable that the great accumulation of uncompacted and not completely waterlogged vegetable debris so characteristic of the Gough Island fern-bush is permitted only because of the relative inefficiency of the soil fauna in its destruction. Detailed studies on the ecology and energy-exchanges of this fauna are much to be desired.

(*c*) *Carnivorous species*

Araneids are the most abundant and widespread carnivorous invertebrates in fern-bush, and are numerically the predominant animals in the *Phylica* canopy. Here their principal food is probably psocids and small nematocerous Diptera, especially chironomids, *Psychoda severini*, and *Bradysia* species, which are abundant. Araneids also abound in the fern-brake, on tree ferns, and in the litter. Owing to incomplete taxonomic study it is not possible to discuss the ecology of the individual spiders.

A red predatory mesostigmatid mite was also common in fern-bush, and was observed to take smaller mites; probably it also feeds on Collembola. The food of the pseudoscorpion, *Chelanops atlanticus*, and the staphylinid beetles, *Quedius* and *Leptacinus* is unknown.

(*d*) *Parasitic species*

Only one parasite is recorded from fern-bush (apart from Mallophaga and ticks associated with the large populations of ground nesting birds). This is the braconid, *Aphidius* cp. *sonchi*, whose distribution is closely correlated with that of the aphids *Neomyzus circumflexus* and *Aulacorthum solani*.

(*e*) *Casual species*

Various adult diptera were encountered generally within the *Phylica* canopy and among the field layer of the vegetation: these were regarded as 'casual' because they showed no particular restriction or correlation with any element in the habitat. The chironomid, *Smittia* sp. and *Psychoda severini* were the most constant and numerous species: nothing is known of their life histories.

The abundant ground-nesting avifauna of fern-bush has a great ecological influence, since most species excavate tunnels in the unconsolidated peat. Swales (1965) points out the very great density of these breeding burrows, and notes that their occupation period may be extended by a phasing of nesting cycles which allows more than one species to use a single breeding site over the year. These sea birds affect the ecosystem chiefly through this mechanical disturbance of the habitat, through enrichment of the soil, and perhaps because of the dispersal opportunities they offer. The galinule, *Porphyriornis nesiotis comeri*, on the other hand, appears to be a generalized feeder and almost certainly takes invertebrates, and the small 'bunting', *Rowettia goughensis*, which feeds in open places in the fern-bush zone and also among the bush canopy, has been seen taking insects as well as seeds. These two land birds are thus partial predators upon invertebrates. The southern skua, *Catharacta skua hamiltoni*, is a common predator on other birds, especially petrels, and the remains of its prey are often to be seen in the fern-bush zone.

TABLE 27. DISTRIBUTION OF FAUNA IN TUSSOCK GRASS AND COASTAL VEGETATION

tussock	tussock with penguins	coastal mixed vegetation at cliff bases
on tussocks and tussock bases		on vegetation
Porcellio scaber	*Porcellio scaber*	*Porcellio scaber*
Folsomia sp.	*Cylindroiulus latestriatus*	*Cylindroiulus latestriatus*
Delphacodes atlanticus	*Tristanomyia frustulifera*	*Coninomus* sp.
Rhopalosipum padi	*Megaselia* sp.	*Aulacorthum solani*
Coninomus sp.	*Psychoda severini*	*Rhopalosiphum padi*
Pentarthrum carmichaeli	*Erioptera holdgatei*	*Dimorphinoctua* sp. larva
Dimorphinoctua goughensis	*Tristania tristensis*	*Tristanomyia frustulifera*
Peridroma margaritosa (larva)		*Parascaptomyza altissima*
Parascaptomyza altissima		*Limosina plumulosa*
Erioptera holdgatei		*Fucellia maritima*
Chelanops atlanticus		*Lucilia sericata*
Araneida spp.		*Limonia medi-atlantica*
tick, sp.		*Psychoda severini*
Succinea flexilis		*Delphacodes atlanticus*
Tristania tristensis		
	on litter, moss and soil	
Porcellio scaber	*Porcellio scaber*	*Porcellio scaber*
Styloniscus australis	*Folsomia* sp.	*Styloniscus australis*
Orchestia scutigerula	*Proisotoma* sp.	*Orchestia scutigerula*
Folsomia sp.	dolichopodid larva	*Cylindroiulus latestriatus*
Cylindroiulus latestriatus	ephydrid pupa	*Monopis crocapitella*
Chelanops atlanticus	tipulid larvae	mites
Oxychilus alliarius	*Erioptera holdgatei*	*Oxychilus alliarius*
Tristania tristensis	mites	
	ticks	

6·22. *Fauna of tussock grassland and coastal fringe vegetation*

Despite their known palatability to mammals (Holdgate & Wace 1961) tussocks of *Poa flabellata* and *Spartina arundinacea* on Gough Island are not heavily attacked by phytophagous invertebrates. The main fauna is to be found among the bases of the tussock, in the interstices of the matted living and dead leaf bases, and in the copious leaf litter between the tussocks. In 'normal' tussock this last habitat contains several species also typical of litter in fern-bush.

Because the majority of penguin (*Eudyptes crestatus*) colonies are sited among tussock grassland, substantial areas of this vegetation are, however, much modified (Wace 1961). In such regions, instead of dry litter and soil occurring between the tussocks, there are areas of wet, highly nitrogenous, trampled mud and here dipteran larvae, mites and ticks are the principal animals. Much the same applies to the rather smaller areas of tussock occupied by breeding fur seals (*Arctocephalus tropicalis*) or breeding and moulting elephant seal (*Mirounga leonina*). All these animals, therefore, affect the ecosystem by their profound

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mechanical effect on the habitat, and by their addition of organic matter to the soil. Burrowing petrels, notably *Puffinus gravis*, are not infrequent in many regions and may further modify the tussock and contribute to soil instability.

Table 27 shows the main invertebrate fauna of 'normal', and 'modified' tussock grassland, and also of the 'cliff base' coastal mixed vegetation. The latter supports rather more phytophagous species than the tussock that was sampled, largely because of the greater predominance in it of *Apium australe* and *Scirpus* spp. As in the fern-bush, the aphids *Aulacorthum solani* and *Rhopalosiphum padi* were taken abundantly on *Apium*, and the parasitic Hymenoptera *Aphidius* cf. *sonchi* and *Nedioptera* cf. *subaptera* were also collected around this plant. *Aulacorthum solani* was once found abundantly on *Cotula goughensis*, as was a single larva of (?) *Dimorphinoctua* sp. *Delphacodes atlanticus* was also far more abundant in this vegetation than in typical tussock, and was present chiefly on *Scirpus*. The small lathridiid, *Coninomus* sp., on the other hand, was very rare. The tineid moth *Monopis crocapitella* was only taken on one pile of dead boughs heavily dunged by penguins. Proximity to the coast certainly accounted for the collection of several diptera (*Fucellia maritima*, *Limosina plumulosa*, *Lucilia sericata*), whose larvae breed either in beach debris or on the carcasses of dead seal and birds which are not uncommon there. It was also responsible for the presence of the supralittoral amphipod, *Orchestia scutigerula*, which occurred up to the summit of Penguin Island, 115 m above the sea.

6·23. *Fauna of upland wet heath*

Table 28 shows the principal species collected in wet heath, at altitudes of from 330 to 825 m above mean sea level. The fauna as a whole is noteworthy for the absence of certain common lowland species, the presence of others characteristic of the uplands, and the overall reduction in number of species which may in part reflect altitude and in part the relative simplicity of the habitat.

Phytophagous species

The molluscs of the genus *Tristania* are far less diverse in wet heath than in the fern-bush. Apart from a few individuals of *T. costellata* taken on tree-ferns in the lowermost station sampled, only *T. tristensis* occurs above the forest line. The alien gastropod *Oxychilus alliarius* is similarly rare in wet heath, being encountered in one station only, at 450 m. Conversely, the endemic *Succinea flexilis* is widely distributed and occurred in almost all the stations worked, being most characteristic of the grass-heath communities at and above the 600 m contour.

Aphids are similarly atypical of the wet heath formation, two species, *Neomyzus circumflexus* and *Jacksonia papillata*, being taken only in one station, at 450 m, among *Scirpus* tufts. Among the beetles, the common lathridiid of the *Histiopteris* fern-brake, *Coninomus* sp., was not found anywhere in the wet heath, but the latter vegetation supports a widespread and characteristic weevil of the genus *Tristanodes*, *T. scirpophilus*. Larvae are common among the bases of *Scirpus* tussock, where they probably feed either on the roots or the stem bases, and pupae were found within the closely appressed sheaths of the leaf bases. Adults are inactive (at least by day) and were taken chiefly among the lower leaf-sheaths of the tufts (Kuschel 1962).

Larvae of noctuid moths, ascribed to an apterous endemic *Peridroma* species and an apterous endemic *Dimorphinoctua* species are also frequently encountered in the wet heath, especially in the grass heath and among *Scirpus* tufts. Both of these species are typical of the uplands, probably feeding among grass roots. Pupation occurs near the ground surface, among the vegetation mat or beneath stones.

Table 28. Fauna of wet heath

on *Blechnum palmiforme*	
Tristania costellata	r
T. tristensis	o
araneid sp.	r
enchytraeid sp.	o
on *Empetrum rubrum* mat	
Tristania tristensis	o
enchytraeid sp.	o
araneids	o
Succinea flexilis	r
Porcellio scaber	r
Styloniscus australis	r
Delphacodes atlanticus	r
on *Scirpus* tufts	
Delphacodes atlanticus	f
Styloniscus australis	f
Tristanodes scirpophilus	o
Chelanops atlanticus	o
predatory mites	o
mites	o
Oxychilus alliarius	r
Dimorphinoctua goughensis	r
Peridroma goughi	r
Peridroma sp. larva	r
araneids	r
Jacksonia papillata	r
Neomyzus circumflexus	r
casual on vegetation	
Ornithomyia remota	
Fannia canicularis	
Parascaptomyza altissima	
tipulid, winged	
Quedius mesomelinus	
Leptacinus sp.	
in soil and stem bases	
Enchytraeus sp.	f
enchytraeid spp.	f
mites	f
Stylonsicus australis	o
Hypogastrura sp.	o
Folsomia sp.	o
lumbricids	o
dolichopodid larva	o
Fredericia sp.	r
dipteran larvae	r
araneids	r
in mixed grass heath	
Tristania tristensis	f
araneids	f
Styloniscus australis	f
Succinea flexilis	o
Tristanodes scirpophilus	o
Delphacodes atlanticus	o
Chelanops atlanticus	o
red predatory mite	o
Dimorphinoctua goughensis	r
Peridroma goughi	r

The other phytophagous species common in wet heath is *Delphacodes atlanticus*, which occurs among *Scirpus* tufts and in grass-heath but rarely attains quite the abundance it does in lowland stations.

Soil and litter species

The most striking feature of the soil fauna of wet heath, in comparison with that of fern-bush and tussock grassland, is the absence of the millipede *Cylindroiulus latestriatus* and the isopod *Porcellio scaber* and the great abundance of oligochaetes. Lumbricids are widely distributed though not strikingly numerous, and enchytraeids are abundant. This change may be connected in some way with a conspicuous alteration in the soil itself, that of the uplands being more compact, more uniform, and having (apparently) a higher mineral content.

Carnivores

In general, the carnivorous species of wet heath resemble those of fern-bush. The araneids are less diverse, being mainly ground-living: among them there appear to be several typically upland species. A predatory red mesostigmatid mite is widespread and numerous, and the false scorpion, *Chelanops atlanticus* was taken once among *Scirpus* bases and once, in numbers, among the appressed lower leaf-sheaths of *Apium australe*.

6·24. *Fauna of montane moorland*

The shallow, wind-eroded soil and thin plant mats of the feldmark have a distinctly scantier fauna than the wet heath (table 29). The phytophagous animals consist only of two gastropods and two noctuid larvae: there are no aphids, weevils, or plant bugs. The soil fauna resembles that of the wet heath in the preponderance of oligochaetes and the absence of millipedes: the soils are in general shallower and more mineral than those even of the wet heath. The predatory fauna is also reduced, consisting of a few spiders and an active red mite.

Table 29. Fauna of montane moorland

Rhacomitrium-Empetrum mats		Stones and soil	
Succinea flexilis	o	Araneida	f
Stylonsicus australis	o	*Styloniscus australis*	f
Peridroma sp. larva and pupa	r	lumbricids, immature	o
Dimorphinoctua sp. larva	r	*Enchytraeus* sp.	o
Agrostis mats		*Henlea* sp.	o
Araneida	f	other Enchytraeidae	o
Tristania tristensis	o–f	*Tristania tristensis*	o
Erioptera holdgatei	o	dolichopodid larva	o
Succinea flexilis	o	dipteran larva	o
Dimorphinoctua sp. larva	o	red predatory mite	r
Peridroma sp. larva	o		
Peridroma goughi adult	r		

6·3. *Range of species*

It is obvious from an inspection of table 25 and the comparison of tables 26 to 29 that a relatively small proportion of the Gough Island fauna is restricted to any given major vegetation type. This conclusion is supported by the data presented in table 30, which sets out the number of species in common between the main formations. It is clear that animals and plants are alike in this lack of restriction, and it might be concluded that the animals, like the plants, are displaying a wide ecological amplitude and occupying a variety of niches.

A considerable degree of this wide range of animal species results, however, from their association with widely distributed plants. The following fairly close associations have been noted in the course of the preceding sections:

Plant	Invertebrate	Dependent invertebrates
Apium australe (also less often, *Scirpus* sp. and *Cotula goughensis*)	*Neomyzus circumflexus*, *Aulacorthum solani*, *Rhopalosiphum padi*	*Aphidius sonchi*, *Nedioptera subaptera*
Scirpus spp. (rarely grasses)	*Delphacodes atlanticus*, *Tristanodes scirpophilus*	
Histiopteris incisa	*Coninomus* sp.	
upland grasses, especially *Agrostis carmichaeli*	*Dimorphinoctua goughensis*, *Peridroma goughi*	
grasses (usually)	*Succinea flexilis*	

The very wide range of *Delphacodes atlanticus* certainly reflects that of *Scirpus*, the bug occurring everywhere with the food plant. *Coninomus* also occurs throughout the range of

Histiopteris. On the other hand, the aphid species are all restricted to the lowland part of the range of *Apium*. It has been suggested by Hille Ris Lambers (1955) that the haploid (summer) generation of aphid may alone be present on Tristan da Cunha and this may also apply to the Gough populations which would in consequence not be frost-hardy. In contrast again, *Tristanodes scirpophilus*, *Dimorphinoctua* sp. and *Peridroma* species are largely restricted to the upland sections of the range of their food plants, and these species, like *Succinea flexilis*, seem to thrive only in open habitats. All of these invertebrates, however, like their food plants, occur in several main formations and a variety of detailed communities.

Table 30. Numbers of plants and invertebrates in common between main formations

(Figure for plants sum of all vascular plants and a few bryophytes of ecological importance (from Wace 1961)—animal totals in italics.)

	tussock	fern-bush	wet heath	montane moor
tussock	33	24	16	13
	39	*25*	*18*	*9*
fern-bush	24	44	25	19
	25	*39*	*24*	*12*
wet heath	16	25	32	19
	18	*24*	*31*	*14*
montane moor	13	19	19	29
	9	*12*	*14*	*17*

Similarly, many carnivores and soil and litter species show a remarkably wide range in formation and altitude. It is more difficult to associate such species with plants, but it is possible that the restriction of *Cylindroiulus latestriatus* to lowland soils, and the replacement of this species by oligochaetes as the main elements in the soil fauna of the uplands, reflects in part the different litter production by fern-bush and wet heath vegetation, as well as a direct altitudinal effect.

6·4. *Comparison with the Tristan group*

The general features of the native ecosystem of Gough Island, described above, probably apply equally to the other Tristan islands, about which insufficient information is available. Brief collections made on Tristan by the present author in October 1955, and on Inaccessible in March 1962 suggest that the fauna of fern-bush and tussock grassland on these islands at least differs little in its salient features from that on Gough. The paucity of phytophagous species on *Phylica* bushes appears to be a general feature, but the faunas of fern-bush on Gough and Tristan do differ in the greater prominence of some aliens (e.g. slugs and centipedes) on the latter, and in the striking absence from Tristan of the lathridiid beetle, *Coninomus*, which is the most abundant insect in this formation on Gough. This last difference may be correlated with the far lower abundance of the fern *Histiopteris incisa* on Tristan, since the beetle seems especially closely associated with this plant.

Collections in tussock grassland in the Tristan islands and in the Falkland Islands in November 1961 suggest that this vegetation type is generally rather poor faunistically and that the Gough fauna is typical in its general features, although naturally more species-poor than in the continental Falklands. While further collecting, and the full taxonomic study of the available collections of Collembola, mites and spiders, all of which are numerous in the Tristan group, will certainly expand the species lists and reveal further details of species distribution between vegetation types in the archipelago, it is thought unlikely that the fauna will emerge as vastly different in features from that described in the present study.

7. The effect of man: the disturbed ecosystem

7·1. *Destruction of native animals*

The first human residents in the Tristan da Cunha group were sealers. In 1790 the American schooner *Industry* took 5600 fur seal (*Arctocephalus tropicalis tropicalis* (Gray)) skins in the northern islands (Allen, in Jordan 1899). By 1810 only about 1000 seal remained in this part of the group (Lambert 1811), while a gang who worked Gough in that year took 1100 skins (Holdgate 1958). By 1829 Gough was virtually worked out (Morrell 1832), but a party which worked there during the resurgence of southern sealing in 1888–89 took 311 seal (Comer, in Verrill 1895). In 1891–92 the last sealing party known to have visited the islands found them deserted. Despite these statements a population nucleus undoubtedly survived, probably on the inaccessible western beaches of Gough and at Inaccessible, and provided the basic stock for the subsequent recovery. The elephant seal (*Mirounga leonina*) populations were also exploited (Lambert 1811), and have made a slower recovery.

Undoubtedly, sealers also directly affected certain sea birds. A party left by the *Baltic* in 1810 obtained 'a great variety of excellent birds' by lighting fires at night (Holdgate 1958) and a party from the *Francis Alleyn* at Gough 1888 'lived on young albatross', had 'about 3000 penguin eggs salted, 1700 in barrels', and also ate 'plenty of albatross eggs' (Comer, in Verrill 1895). The first settlers on Tristan in 1810 followed a similar pattern of exploitation. Their leader, Jonathan Lambert, writing in 1811 mentions killing elephant seal, fur seal, and the endemic moorhen and proposed to establish an industry to exploit the seals and also the sea birds for feathers. Since that time the continued depredations of the islanders, aided by the ground predators they imported deliberately or inadvertently (dogs, cats, pigs, and rats), have greatly reduced the avifauna of Tristan (Elliott 1953, 1957). *Diomedea exulans* has been eliminated as a breeding species from Tristan and reduced to a tiny remnant on Inaccessible, and *D. chlororhynchos* and *Phoebetria fusca* definitely reduced. The majority of the ground-nesting petrels of the main island have been reduced to very small remnant populations or even eliminated. The endemic moorhen, *Porphyriornis nesiotis nesiotis*, and the endemic 'canary', *Nesospiza acunhae acunhae* are both extinct on Tristan. Penguins (*Eudyptes crestatus*) maintain only small populations on the least accessible parts of the main island although their numbers, like those of the ground-nesting sea birds and endemic land birds, remain great on the other islands to which predators have not so far been imported.

7·2. *Modification of habitat*

The clearing of the Settlement Plain at Tristan (Holdgate & Wace 1961; Wace & Holdgate 1958) and burning of this and other areas, coupled with the importation of grazing mammals and alien plants, have substantially modified the habitat over large areas of the main island and smaller areas of Inaccessible, Nightingale and Gough. In these disturbed areas where alien plants have established themselves and formed new vegetation types, the invertebrate fauna has been substantially changed. The destruction of ground-nesting petrel populations has probably also had a large indirect effect, since these birds formerly both disturbed and manured the ground: new soil types have probably appeared on their former breeding grounds and these may have been further influenced by the activities of imported soil invertebrates such as lumbricid worms.

7·3. *Importation of alien species*

Man has deliberately imported domestic stock (donkeys, cattle, sheep, pigs, geese, fowls and formerly goats) to Tristan, and some of these (cattle, pigs, and sheep) to Inaccessible. Sheep and goats, as well as fowls, have recently been imported to Gough Island. Appreciation of the dangers of such introductions has fortunately led to the elimination of sheep and goats from Gough, while the alien mammals imported to Inaccessible have now died out. On Tristan, however, grazing mammals have almost certainly contributed to the elimination of tussock grassland (Holdgate & Wace 1961). Feral cattle (themselves worthy of detailed study because they show variations in habits and conformation from present domestic stock) now range the Stony Hill area of Tristan, while domestic cattle, donkeys and some sheep remain on the Settlement Plain and there may be a few sheep on the Peak also.

Among predators, dogs and cats deliberately imported by man have done serious damage to the avifauna of Tristan, on which island cats are now feral. At present *Felis domesticus* L. is widespread but nowhere very abundant. More serious damage has probably been done by rats (*Rattus rattus*, with two subspecies represented (Hill 1959)), which abound on Tristan but have fortunately reached no other island. The first introduction of these animals is said to have occurred in 1882, when the *Henry B. Paul* was wrecked. The extermination of the endemic Tristan gallinule, *Porphyriornis nesiotis nesiotis* and the Tristan population of the 'canary', *Nesospiza acunhae*, as well as the catastrophic reduction in the marine avifauna has been blamed on rats, although the feral cats probably played a contributory part as they did on Ile Nouvelle Amsterdam (Holdgate & Wace 1961; Dorst & Milon 1964). Mice (*Mus musculus* L.) have also become established on Tristan and Gough, probably arriving with the first sealers. On Gough Island they abound from sea-level to the highest summits and on Tristan they ascend at least to the Base. The Gough Island population of mice consists of rather large individuals, which also show colour differences from a typical European sample but cannot be regarded as subspecifically or varietally distinct at present (Hill 1959). This feral population appears to have adopted a typical 'field mouse' niche, but readily re-assumed a semi-domestic habit when the island became inhabited in 1955 (Holdgate 1958). The mice seem to have had no harmful effect on the native ecosystem, but their precise role awaits further study.

Numerous alien invertebrates have been imported, and as table 19 shows, they are concentrated especially on Tristan where they almost outnumber the native fauna. Gough, with nineteen species, has the next largest total, but under-collecting on Inaccessible and Nightingale may be reflected in this pattern, since the latter islands have received at least as much human disturbance as Gough. In a few cases the arrival of these aliens is documented. The willow aphid, *Tuberalachnus salignus* was first collected in 1956 after young trees had been imported. The weevil *Pantomorus cervinus* was seen in 1955 in the boats and the Settlement after a load of hay had been landed. The carabid, *Harpalus agilis* and the coccinellid, *Adalia flavomaculata* have almost certainly arrived since 1956. Slugs and centipedes, common on Tristan in 1955–56 were carried accidentally to Gough at that time and may now be spreading there. Many other aliens whose arrival is less well documented are concentrated in the Settlement and cannot be held fully established. The beetles *Sitophilus oryzae*, and *Ahasverus advena* from Tristan, and *Hylergus ligniperda* and *Henoticus californicus* from Gough are in this category. Other aliens, like most of the centipedes and millipedes, are still most abundant in modified habitats near human habitation, but a substantial element (e.g. the millipede *Cylindroiulus latestriatus*, the gastropod *Oxychilus alliarius*, the isopod *Porcellio scaber*, several lumbricid worms, numerous diptera and several Coleoptera) are well established in natural habitats on more than one island.

Comparison of the lists of species recorded in the natural vegetation of Gough, set out above, with those for disturbed vegetation on the Tristan Settlement plain, listed by Baird (1965: Part V, this report), demonstrates these points clearly. Undoubtedly the present position is not static: as time goes on, more aliens will be imported and some will spread, while species will continue to be carried from Tristan to the other islands of the group. The relative successes of these aliens, and the degree to which their establishment is restricted to habitats first opened for them by human interference, demands more critical study.

7·4. *Increased interchange between islands*

For over a century the residents of Tristan have made regular boat journeys between the three northern islands, carrying stores, plants, and sometimes stock. Since 1948 annual or more frequent voyages have been made by fishing ships between Tristan and Gough. These inter-island journeys undoubtedly increase the chance of spread of a species throughout the group and may have contributed to the wide ranges of certain native and alien invertebrates. Kuschel (1962) even considered whether such an importation could explain the anomalous distribution of *Tristanodes scirpophilus* on Tristan and Gough, but concluded this was unlikely in this particular case.

Appendix B. The terrestrial fauna of the Tristan–Gough group

(Compiled from available published and unpublished sources)

group	species	islands	category
Platyhelminthes			
Procerodidae	*Procerodes ohlini* (Bergendal)	G	3
Nemertea			
Prosorhochmidea	*Geonemertes nightingaleensis* Brinckmann	T I N	2
Annelida			
Lumbricidae	*Allolobophora* cp. *chlorotica*	T	5
	Bimastus cp. *eiseni*	T	5
	Lumbricus rubellus	T	5
	cp. *Eisenella tetraedra*	T	5
	gen. et. sp.?	T G	5?
Enchytraelidae	*Enchytraeus australis* Stephenson	G	3
	Enchytraeus sp.	G	4
	Fridericia sp.	T G	4
	Henlea sp.	G	4
	Lumbricullus sp.	G	4
Acanthodrilidae	cp. *Plutellus* or *Diplotrema* sp.	G	3?
Mollusca			
Succineidae	*Succinea flexilis* Quick	G	1
	Succinea sp. (Odhner, in prep.)	T, etc.?	1 or 2
Zonitidae	*Oxychilus alliarius* (Miller)	T G	5
Clausiliidae	*Tristania tristensis* (Gray)	T I G	2
	T. ventricosa (Gray)	T G	2
	T. costellata Odhner	T G	2
	T. costigera Odhner	T G	2
	T. goughensis Odhner	G	1
	T. flavida Odhner	G	1
Limacidae	*Milax gagates* (Draparnaud)	T G?	5
	Agriolimax reticulatus (Müller)	T G?	5
Crustacea			
Ostracoda	*Cypridopsis* sp.	T	3?
Amphipoda	*Orchestia gammarellus* Pallas	T	3
	O. platensis Kroyer	T I G	3
	O. scutigerula (Dana)	I N G	3
Isopoda	*Iais pubescens* (Dana)	G	3
	Porcellio scaber Latr.	T G	5
	Styloniscus australis	T G	2
Myriapoda			
Blaniulidae	*Blaniulus guttulatus* (Bosc.)	T	5
Iulidae	*Cylindroiulus latestriatus* (Curtis)	T I N G	5
	Brachyiulus pusillus (Leach)	T I	5
Geophilidae	*Necropholcophagus longicornis* (= *Geophilus tristanicum* (Attems), *G. dacunhae* Lawrence)	T	5
Henicopidae	*Lamyctes fulvicornis* Meinhert, (= *L. tristani* (Pocock))	T	5
Lithobiidae	*Lithobius melanops* Newport, (= *L. hageni* Lawrence)	T I G	5
	Lithobius sp.	T	5
Insecta			
Thysanura	gen. et. sp.	T G	4
Collembola	*Hypogastrura delicatula* Lawrence	T	4
	Hypogastrura armata (Nicolet)	G	4
	Hypogastrura sp.	G	4
	Isotoma notabilis Schäfer	G	4
	Isotoma sp.	G	4
	Folsomia sp.	G	4
	Proisotoma minuta (Tullberg)	G	4
	Proisotoma sp.	G	4
	Megalothora sp.	G	4
	Sminthinurus sp.	G	4
	Entomobrya multifasciata Tullberg	T	4
	Entomobrya nivalis L.	G	4

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APPENDIX B (*cont.*)

group	species	islands	category
Orthoptera	*Tridactylus subantarcticus* Willemse	T	1
Dictyoptera	Blattidae, gen. et. sp. indet.	T	5
Odonata	gen. et. sp. ?	?	3*
Psocoptera	*Atropos pulsatoria* (L.)	T	5
	Cerobasis annulata (Hagen)	G	4
	Lepinotus inquilinus (Heyden)	G	5
	Ectopsocus briggsi McLachlan	G	4
	Troctes pubescens (Broadhead)	T	5
	gen. et. sp. ?	I	4
Hemiptera: Homoptera	*Delphacodes atlanticus* China	T I N G	3
	Aulacorthum solani (Kalt.)	G	4
	Neomyzus circumflexus (Duckton)	T I G	4
	Myzus persicae (Sulzer)	I	4
	Rhopalosiphum rufiabdominalis (Sasaki)	I	4
	R. padi (L.)	N G	4
	Jacksonia papillata	G	4
	Tuberolachnus salignus (Gmelin)	T	5
	Cavariella aegopodii (Scop.)	T	4
	Hemiberlesia rapax (Comstock)	T I	5
Hemiptera Heteroptera	*Calocoris norvegica* (Gmelin)	T	5
	Lyctocoris campestris (Fabricius)	T	5
	Cimex lectularius (L.)	T	5
	Nabis hageni China	I N	2
	Pentatomidae, gen. et. sp. ?	T	5
Thysanoptera	*Thrips tabaci* Lindeman	I	5
	Nesothrips inaccessiblensis Morison	I	1
Lepidoptera	*Endrosis sarcitella* (L.)	G	5
	Agonopterix goughi Bradley	G	1
	Hofmannophila pseudospretella Stain.	T	5
	Plutella xylostella Schrank	T I	5
	Monopis crocicapitella Clemens	G	5
	Niditines spretella Schiff.	T	5
	Ephestia kuhniella Zeller	T	5
	Udea hageni Viette	T	1
	Nycterosea obstipata (Fabr.)	T N	3
	Euxoa costalis (Walker)	T	3
	Agrotis segetum Schiff.	T	5
	Dimorphinoctua pilifera Walker	T I N	2
	D. cunhaensis Viette	T I N	2
	Dimorphinoctua goughensis Fletcher	G	1
	Peridroma porphyrea (Schiff.)	T I G	4
	Peridroma goughi Fletcher	G	1
	Protoleucania exoul (Walker)	T I N	2
	Othreis apta (Walker)	T G	3*
	Mocis punctularis Hübner	T	5
	Otosema odora (L.)	T I	3*
	Vanessa braziliensis Moore	T	3*
	Herse cingulata F.	T	4
Hymenopter	*Aphidius* cp. *sonchi*	G	4
	Nedioptera cp. *subaptera*	G	4
	Phygadeuon sp.	T	4
Coleoptera	*Bidessonotus involucer* Brinck	I G	2
	Lancetes varius (F.) *dacunhae* Brinck	T I G	(3) 2
	Senilites tristanicola Brinck	I N	2
	Cercyon litoralis Gyll.	I	4
	C. depressus Steph.	T I	4
	Ptinella natvigi Brinck	I	1
	Oxytelus christopherseni Brinck	T	4
	Quedius mesomelinus Marsh.	T I N G	4
	Quedius fulgidus F.	N	5
	Leptacinus sp.nov. ?	G	1 ?
	Leptacinus sp.	T	4
	Atheta cp. *laticollis* (Steph.)	T I N	3 ?

APPENDIX B (*cont.*)

group	species	islands	category
Insecta (*cont.*)			
Coreoptera (*cont.*)	*Harpalus agilis* Peringuey	T	5
	Adalia flavomaculata de Geer	T	5
	Ahasverus advena (Waltl.)	T	5
	Stegobium paniceum L.	T	5
	Cartodere filum (Aube)	T	5
	Corticaria serrata (Payk)	I	5
	Coninomus sp.nov. Balfour Browne	G	1
	Hylurgus ligniperda (Fabr.)	G	5
	Henoticus californicus (Mann)	G	5
	Cryptophagus dentatus (Hbst.)	G	5
	Nacerda melanura (L.)	T	5
	Sitophilus oryzae (L.)	T	5
	Stenoscelis hylastoides Woll.	T	4
	Pentarthrum carmichaeli Waterh. (= *P. tristanensis* Brinck)	T I N G	2
	Pantomorus cervinus (Boh.)	T	5
	Phlyctinus callosus Boh.	T	5
	Palaechtus glabratus Waterh.	N	1
	Palachtodes cossonides (Waterh.)	I N	2
	Innacodes oblongus Brinck	I	1
	Gunodes major Brinck	N	1
	Tristanodes integer Brinck	I	1
	T. silvertseni Brinck	N	1
	T. attai Brinck	T	1
	T. medius Brinck	I	1
	T. minor Brinck	N	1
	T. repettonis Brinck	I	1
	T. conicus Brinck	I	1
	T. echinatus Brinck	I	1
	T. insolidus Brinck	N	1
	T. scirpophilus Brinck	T G	2
	T. craterophilus Brinck	T	1
Diptera: Nematocera	*Limonia medi-atlantica* Freeman	T G	2
	Erioptera holdgatei Freeman	G	1
	Psychoda severini Tonnoir	G	5
	Bradysia mycorum Frey	T I	5
	Bradysia spp. indet.	G	5
	Cosmosciara perniciosa Edwards	T N	5
	Clunio africanus Hesse	G	3
	Telmatogeton sancti-pauli Schiner	T G	3
	Smittia sp.	G	3
	cp. *Parakiefferiella* sp.	T	4
Diptera: Brachycera	*Hydrophorus carmichaeli* Walker	T N	2
	H. tristanensis Walker	T I	2
	H. christopherseni Frey	T I N	2
	Piophila casei L.	T	5
	Scaptomyza horrida Frey	I	1
	S. brevilamellata Frey	N	1
	S. pectinifera Frey	I N	2
	S. incerta Frey	I	1
	S. angustinennis Frey	N	1
	S. altissima Frey	T I N G	2
	S. helvola Frey	T I N	2
	S. freyi Hackman	N	1
	S. frustulifera (Frey)	N G	2
	Drosophila punctatonervosa Frey	T	4
	D. simulans Sturt	T N	5
	Leptocera abdominiseta Duda	T	3
	Leptocera sp. indet.	T	3
	Thoracochaeta seticosa Spuler	T N	3
	T. brachystoma Stenh.	T I N	3
	T. zosterae Haliday	G	3

APPENDIX B (*cont.*)

group	species	islands	category
Diptera: Brachycera (*cont.*)	*Limosina plumulosa* Rondani	G	3
	L. subbrevipennis Frey	N	1
	L. heteroneura Haliday	T I	3
	Dimecoenia tristanensis Frey	T I N G	2
	Dimecoenia sp. indet.	I	4
	Centromeromyia eremita Frey	N	1
	Meoneura sp. indet.	G	4
	Megaselia sp. indet.	G	4
	Fucellia maritima Haliday	T I N G	3
	Fannia canicularis L.	T I N	5
	Muscina stabulans Fallen	T	5
	Musca domestica L.	T	5
	Coenosia humilis Meigen	T	5
	Calliphora vomitoria L.	T G	5
	Lucilia sericata Meigen	T I N G	5
Arachnida: Pseudoscorpionida			
	Chelanops atlanticus Beier	T I G	2
Acarina	*Phthiracarus* sp.	G	3
	Pergamasus sp.	T G	3
	Argas sp.	T	3
	Linopodes sp. cp. *motatorius*	T	3
Araneida	*Tegenaria domestica* (Cl.)	T	5
	Achaearanea tepidariorum (C.L. Koch)	T	5
	Teutana grossa C.L. Koch	T	5
	Ostearius melanopygius (O.P.C.)	T	5

(many other species, including 2 *Steatoda* spp., 1 *Philodromus* sp. and 5 Liniphiid species, represented in collections)

PARASITIC INVERTEBRATE SPECIES

group	species	host
Mallophaga	*Austrogoniodes cristati* Keler	*Eudyptes crestatus*
	Perineus diomedeae (Fabricius)	*Diomedea* and *Phoebetria* spp.
	P. obscurus (Rudow)	*Macronectes giganteus*
	Docophoroides brevis (Dufour)	*Diomedea exulans*
	D. simplex (Waterson)	*D. chlororhyncos*
	D. hunteri Harrison	*Macronectes giganteus*
	Harrisoniella ferox (Giebel)	*Diomedea melanophris*
	Naubates prioni (Enderlein)	*Pachyptila forsteri*
	Naubates harrisoni Bedford	*Puffinus gravis*
	Halipeurus abnormis (Piaget)	*P. gravis*
	Trabeculus schillingi Rudow	*Pterodroma mollis*
	Longimenopon galeatum Timmermann	*Pelagodroma marine*
	Pseudomenopon rowani Keler	*Atlantisia rogersi*
	Rallicola sumpti (Keler)	*A. rogersi*
	Quadraceps houri Hopkins	*Sterna vittata*
	Saemundssonia sterni (L.)	*S. vittata*
	S. lockleyi Clay	*S. vittata*

(further undetermined material of several genera exist)

group	species	islands	category
Siphonaptera	*Pulex irritans* L.	T	5 (settlement, on man only)
	Parapsyllus longicornis dacunhae de Meillon		2 (*Puffinus gravis* and *Nesocichla eremita gordoni*)
	P. l. longicornis		3 (*Diomedea chlororhynchos*)
Hemiptera	*Cimex lectularius*	T	5 (on man)
Diptera	*Ornithomyia remota* Walker	N G	3 (from *Porphyriornis nesiotis comeri*, *Rowettia goughensis*, *Nesocichla eremita* and *Nesospiza wilkinsi*)
Acarina	*Ixodes percavatus* Neumann	T I N	2 (several birds)
	Ixodes sp. indet.	N	4
	Boophilus decoloratus (Koch)	T	5 (uncertain)

(various undetermined species from Gough Island)

APPENDIX B (*cont.*)

group	species	islands	category
Aves	*Aptenodytes patagonicus* Miller	G	7
	Eudyptes chrysolophus (Brandt)	I	7
	E. crestatus moseleyi Math. & Iredale	T I N G	6 (2)
	Oceanites oceanicus (Kuhl)		
	Garrodia nereis (Gould)	G	6
	Fregetta grallaria melanoleuca (Salvad.)	I N G ?T	6 (2)
	Pelagodroma marina (Lath.)	I N G	6
	Puffinus assimilis elegans Gigl. & Salvad.	I N G ?T	6 (2)
	P. gravis O'Reilly	I N G	6 (2 ?)
	Adamastor cinereus (Gmel.)	T G I?	6
	Fulmarus glacialoides		7
	Procellaria aequinoctialis (L.)		6/7
	P. aequinoctialis conspicillata (Gould)	I	6
	Pterodroma macroptera (Smith)	T G	6
	P. incerta (Schlegel)	T G	6
	P. mollis (Gould)	T I N G	6
	P. brevirostris (Lesson)	G I? N?	6
	P. externa Salvin		7
	Daption capensis (L.)		7
	Pachyptila vittata (Gmel.)	T I N G	6
	Macronectes giganteus (Gmel.)	G	6
	Pelecanoides urinatrix dacunhae Nicoll, *P. u. elizabethae* Elliott	I N G	6 (2)
	Diomedea exulans exulans L.		7
	D. exulans dabbenena Math.	I G	6 (2)
	D. melanophris Temm.		7
	D. chlororhynchos Gmel.	T I N G	6
	Phoebetria fusca (Hils.)	T I N G	6
	P. palpebrata (Forster)	G	7
	Egretta thula Molina	T	3*
	Atlantisia rogersi Lowe	I	1
	Porphyriornis nesiotis comeri Allen	G	(2) 1
	Porphyrula martinica L.	T	3*
	Charadrius modestus (Licht)	T	3*
	Bartramia longicauda Bechts.	T	3*
	Actitis macularia L.	T	3*
	Tringa acuminata (Horsf.)	T	3*
	Larus dominicanus Licht.		7
	L. pipixcan Wagler	G	7
	Catharacta skua hamiltoni Hagen	T I N G	6
	Sterna macrura Naum.		7
	S. vittata tristanensis Murphy	T I N G	6
	Anous stolidus stolidus (L.)	T I N G	6
	Nesocichla eremita eremita (Gould)	T	(2) 1
	N. eremita gordoni Stenhouse	I	(2) 1
	N. eremita procax Elliott	N	(2) 1
	Hirundo rustica erythrogaster Bodd.	T	3*
	Nesospiza acunhae acunhae Cab.	(T) I	(2) 1
	N. acunhae questi Lowe	N	(2) 1
	N. wilkinsi wilkinsi Lowe	N	(2) 1
	N. wilkinsi dunnei Hagen	I	(2) 1
	Rowettia goughensis (E. Clarke)	G	1
Mammalia			
Rodentia	*Rattus rattus alexandrinus* (Desmarest)	T	5
	R. rattus frugivoris (Rafinesque)	T	5
	Mus musculus L.	T G	5
Carnivora: Pinnipedia	*Arctocephalus tropicalis tropicalis* (Gray)	T I N G	6
	Mirounga leonina (L.)	T I G	6
Fissipedia	*Felia domesticus* L.	T	5

Explanation of column 4:

1, species endemic to one island;
2, species endemic to island group;
3, species native to island group;
3*, naturally occurring straggler, not established in group;
4, species of doubtful status;
5, introduced species;
6, marine bird or mammal, breeding in group;
7, marine bird or mammal, visiting Tristan waters.

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