# SPECIES - AREA AND SIMILAR RELATIONSHIPS OF INSECTS AND VASCULAR PLANTS ON THE SOUTHERN OUT LYING ISLANDS OF NEW ZEALAND

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SUMMARY: Relationships of species numbers to island biogeographic variables (area, altitude, distance from source pool) have been studied for indigenous lepidoptera, diptera, coleoptera and vascular plants inhabiting seven of New Zealand's outlying islands to find the best statistical model for the linear relationship between species number and each of the biogeographic variables and for that between the insects and plants. Percentage of variance accounted for by the regressions was used as the criterion for best-fit.

For the species-area relationship and that between the insects and plants the best model was that using untransformed data; for the species-distance and species-altitude relationships only the log/log model for the plant species-altitude relationship yielded a statistically-significant value for the correlation coefficient.

Though there are significant correlations between island areas and the number of species per genus of both insects and vascular plants they support, this is not accepted as evidence for competitive exclusion. Simberloff's views (1970, 1978) on the subject are discussed and attention is drawn to the land arthropod fauna of the Bounty Islands in which there are 17 species each belonging to a different family.

## INTRODUCTION

This paper is concerned with two allied aspects of the mathematical relationships between the number of species living in insular places and certain geographical parameters: (i) the classic species number-island area relationship (and its close relatives involving altitude and degree of isolation) and (ii) the species diversity-area relationship, diversity in this instance being measured by the species / genus ratio.

Although there have been numerous studies-some highly sophisticated-of the mathematical relationships between the number of species living on islands and certain geographical parameters such as area, altitude and distance from the species' source, no convincing explanation has yet emerged to account for the simple linear result so frequently and widely reported (e.g. Fig. 2). However, there now seems to be increasing agreement that the MacArthur and Wilson (1967) treatment of the species-area relationship, upon which their equilibrium theory is based, errs in assuming the generality of its expression by the function $S=cA^z$, in which S is the number of species, A is the insular area and c and z are constants (c being the intercept of the regression on the Y axis and z the slope of the regression). MacArthur and Wilson proposed, furthermore, that each of the constants might eventually be shown to have biological significance.

In the first part of this paper the four mathematical models discussed by Connor and McCoy (1979) are examined to determine which best fits the species-area and other species number-based relationships of some native insect groups of the southern outlying islands of New Zealand, and I have taken the opportunity to do the same for the native vascular plants upon which the insects must, to a large extent, ecologically depend. The investigation has been made to see if the results confirm those of Connor and McCoy, i.e. one cannot assume, as MacArthur and Wilson have done, that the log/log (or power) function is the model invariably giving the best fit.

In the second part of this paper, and using the same basic data, the relationship between the area of islands and the mean number of species per genus found upon them is examined in the New Zealand context and in the light of Simberloff's (1970) criticism of the assumption that the diminishing value of S / G ratio with diminishing island area is evidence for the operation of competitive exclusion.

In some ways the islands of the New Zealand region are not ideal for the study of numerical aspects of island biogeography. Firstly, there is a wide size-gap between the two largest land masses (South Island, $1.50 \times 10^5$ km²; North Island, $1.15 \times 10^5$ km²) and the other "mainland" island (Stewart Island, $1.75 \times 10^3$ km²); there are no land-bridge islands larger than 300 km² (Great Barrier) and no outlying island
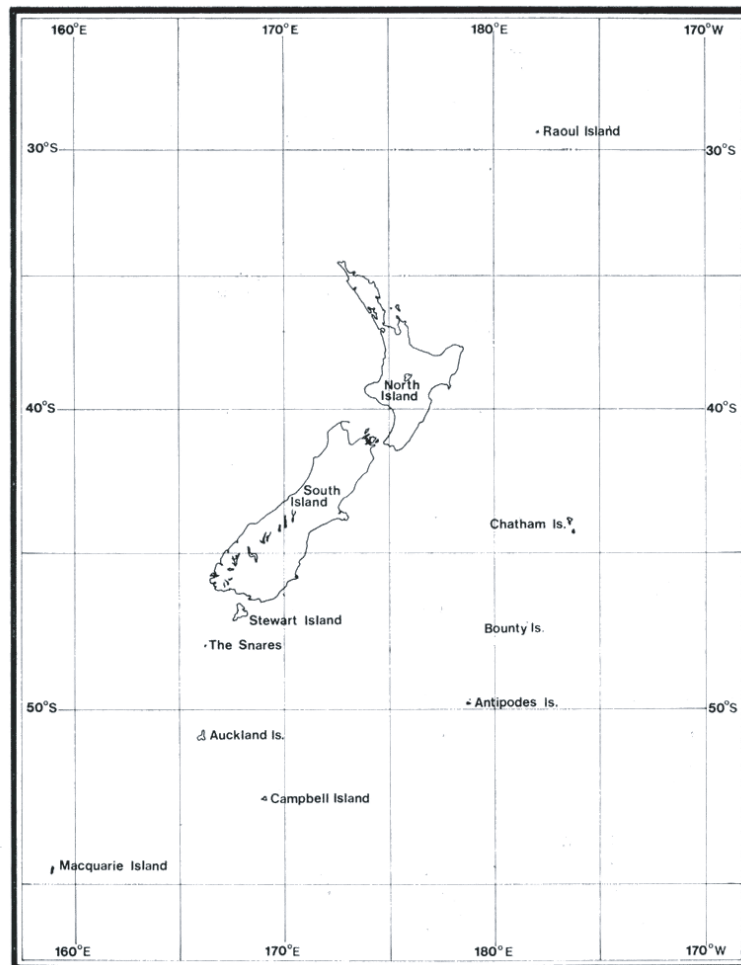
FIGURE 1. *The outlying islands of the New Zealand region.*

larger than 900 km$^2$ (Chatham Island). Secondly, the main axis of the archipelago lies roughly NE to SW over some 4000 km or 34 degrees of latitude; thus there is a climatic cline of subtropical to sub-antarctic from Raoul Island at 20°15'S to Macquarie at 54°30'S (Fig. 1). On the other hand, for many of the islands, particularly the outlying ones, frequent surveys during the last 25 years or so have produced comprehensive faunal and floral lists. With the possible exception of the Chatham Group, extinction is unlikely to have been significant as far as insects and vascular plants are concerned. There is no information that would allow a reliable estimate to be made of turnover rates of species of insects or plants; such information as there is of species being recorded on earlier occasions but not found later could refer to vagrants, mis-identifications or inaccurate locality records. However, the more precise data obtained on recent surveys should, in future, prove useful in establishing the extent to which the turnover of species occurs.

## THE ISLANDS AND THE SPECIES

The southern outlying islands have been chosen for this investigation because they support relatively simple ecosystems with limited insect faunas and vascular floras which, with the exception of those of the Chathams, have been intensively studied and the results published over about the last 20 years.

The lepidoptera, diptera and coleoptera have received not only the most attention of all the insect orders and so are the most fully known, but they
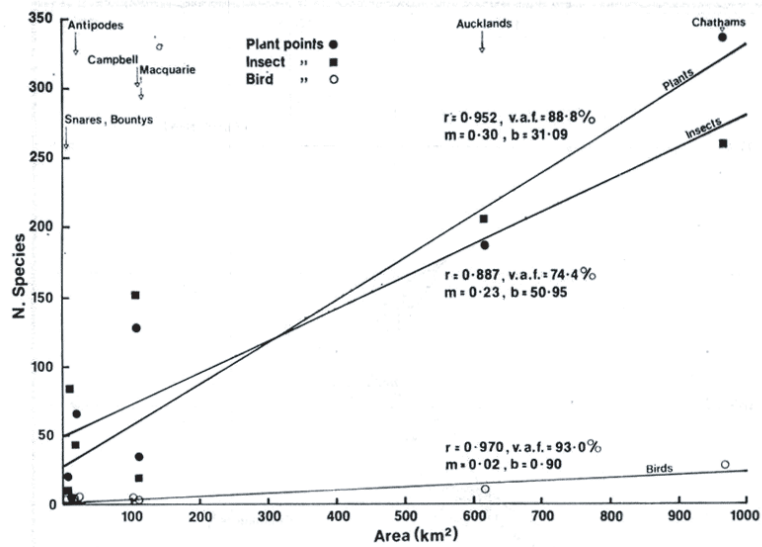
FIGURE 2. *Species number—island area regression for the southern outlying islands of the New Zealand region.*

are conveniently numerous as well and the lists of vascular plants are probably substantially complete. The taxonomy of both groups is now well established though many of the coleoptera of the Chathams, which were described by Broun, need re-examination (Watt, 1982). As complete species lists of insects and vascular plants are, with few exceptions, not readily available for islands other than the southern ones, comparisons between off-shore (land-bridge) islands and outlying islands, such as have been made with birds (Williams, 1981), are not practical at present.

Because the number of species reported from an island may reflect the number of investigatory visits made to it (Connor and Simberloff, 1978) the following information is relevant: The Chatham Islands, continuously occupied for hundreds of years by Polynesians, were colonized by Europeans in the mid-nineteenth century since when they have been farmed and frequently visited by scientific expeditions of various kinds. The remaining islands have not been continuously occupied, or regularly visited, until comparatively recently. Campbell Island was used as a sheep run from about 1895 to 1931, has been the site of a small manned meteorological station since 1941 and has been biologically well surveyed. On the main island of The Snares, a biological research station, established in 1961, has been used regularly since, usually in summer, and Mac-

quarie Island has had a biological and meteorological station since 1948. The Bountys, Antipodes and Auckland Islands have been visited by numerous scientific expeditions, especially since 1950, though the Bountys, because they are so exposed and inhospitable, have received the least attention.

General accounts of the islands may be found for the Antipodes in Warham & Johns (1975); for the Aucklands, Bountys, Campbell and Snares in Gressitt (1971); for the Chathams in Richards (1952) and for Macquarie in Gressitt *et al.* (1962). Only the Chathams, Snares and Aucklands support forest; Campbell has some scrub; the Antipodes and Macquarie are tussock-covered but the Bountys are bare rocks.

As far as the insect species lists are concerned, in the absence of any recent comprehensive publications dealing with the Chatham Islands, I have been fortunate in having access to an up-to-date list of their lepidoptera (Macfarlane, pers. comm.) and have been able to supplement Broun (1908, 1909, 1910) and Brookes (1925) on the coleoptera and Miller (1950) on the diptera with papers by Macfarlane (1979), Watt (1980) and Harrison (1959). There is reason to believe that knowledge or publication of the dipteran fauna is less complete than that of the other two orders-not only are there 10 families occurring further south that are apparently not yet reported from the Chathams (including the Mycetophilidae

TABLE 1. *The southern outlying islands of the New Zealand region. General data.*

| Island or Group | Total land area (km²) | | Distance (i) from N.Z. (ii) nearest neighbour (km) | Altitude (m) | N Lepidoptera | N Diptera | N Coleoptera | N (Total) Insects | N Vascular plants |
|---|---|---|---|---|---|---|---|---|---|
| Chatham 44∞S | 965 | (i) (ii) | 645 515 | 282 | 87 | 61 | 111 | 259 | 335 |
| Bounty 47° 40'S | 1.3 | (i) (ii) | 650 220 | 89 | 2 | 7 | 3 | 12 | 0 |
| Snares 48∞S | 2.8 | (i) (ii) | 105 105 | 189 | 8 | 49 | 25 | 82 | 18 |
| Antipodes 49∞ 40'S | 21 | (i) (ii) | 730 730 | 402 | 9 | 25 | 9 | 43 | 66 |
| Auckland 50∞ 40'S | 612 | (i) (ii) | 370 275 | 645 | 39 | 110 | 57 | 206 | 187 |
| Campbell 52° 30'S | 114 | (i) (ii) | 590 270 | 569 | 28 | 84 | 40 | 152 | 128 |
| Macquarie 54∞ 30'S | 118 | (i) (ii) | 1100 600 | 422 | 1 | 15 | 4 | 20 | 35 |

and Chironomidae), but only for there is the number of reported diptera less than that for lepidoptera and coleoptera combined (see Table 1.).

For compiling the lists for the other islands I have depended on Dugdale (1973, 1975), Farrell (1975), Gaskin (1975), Gressitt *et al.* (1962, 1964, 1971), Harrison (1976), Horning (1976, 1977), Horning and Horning (1974, 1975), Hudson (1975), Johns (1974, 1975), Johnson (1975), Ordish (1974), Spencer (1976, 1977), Suble'te and Wirth (1980) and Watson (1967) in addition to other references already cited. The full lists of species are held in the Department of Entomology, Lincoln College.

The plant lists were compiled from the following: Godley in Anon. (n.d.) for the Antipodes Islands; Johnson & Campbell (1975) for the Aucklands; Given & Meurk (1980) for Campbell Island; Allan (1961), Moore and Edgar (1970), D. R. Given and P. Williams (pers. comm.) for the Chatham Islands; Gressitt *et al.* (1962) for Macquarie; and Fineran (1969) for The Snares. The Bounty Islands support no vascular plants.

Table 1 incorporates the basic data for the various islands. Nearest neighbour distances, although included, do not yield correlations as good as those obtained from using distance from source, and those involving latitude are such that they also have not been pursued. Connor and Simberloff (1978) have discussed reasons why we should not be surprised at these results.

## COMPUTER PROGRAM

The computer program used in this investigation was GENSTAT V Mark 4.03 designed by Lawes Agricultural Trust, Rothamsted Experimental Station.

## RESULTS

*The speciesÖarea relationship*

As Connor and McCoy (1979) have explained, four statistical models are available to express this relationship: (i) the power function (or double log transformation), (ii) the exponential (or species-log area transformation), (iii) the log species-area transformation and (iv) that using untransformed data. The mathematical significance and relevance to island biogeography of each of these is explained by Connor and McCoy; all I have done in this paper is to compare the results given by each for the local situation and so determine which is the best model. Connor and McCoy took the best to be that which had a correlation coefficient at least 5 % better than any of the others. I have used the best value for the percentage of variance accounted for by the regression, as calculated by GENSTAT (Alvey *et al.*, 1980).

Keeping in mind (a) the small number of islands and (b) the range of areas involved (extending over only three orders of magnitude), the best model for the insects and the plants is that using the untransformed variables (Table 2). Among the insect orders, the diptera are an exception but this may be because the number of species recorded from the Chathams

TABLE 2. *Analysis of the number of species vs island area for three insect orders and vascular plants on outlying islands of New Zealand, using the models discussed by Connor and McCoy (1979).*

| | | MODEL TESTED | | | |
| | | Spp./ area | Spp./ log area | Log spp./ area | Log spp./ log area |
|---|---|---|---|---|---|
| Lepidoptera | r | 0.943 | 0.738 | 0.737 | 0.625 |
| | v.a.f.* | 86.8 | 45.4 | 45.1 | 26.8 |
| Diptera | r | 0.541 | 0.630 | 0.537 | 0.645 |
| | v.a.f. | 15.1 | 27.6 | 14.6 | 29.7 |
| Coleoptera | r | 0.934 | 0.719 | 0.751 | 0.659 |
| | v.a.f. | 84.8 | 42.0 | 47.7 | 32.1 |
| All the above | r | 0.887 | 0.770 | 0.710 | 0.694 |
| | v.a.f. | 74.4 | 51.1 | 40.4 | 37.9 |
| Plants | r | 0.952 | 0.833 | 0.570 | 0.831 |
| | v.a.f. | 88.8 | 63.3 | 19.0 | 62.8 |

\* % variance accounted for by the regression, as calculated by the GEN-
   STAT program.
p = 0.05 r = 0.754; p = 0.01 r = 0.874.

is incomplete. The values of r calculated from the untransformed data are significant at the 1 % level or better, except that for the diptera.

It is possible that had a greater range of island areas been involved, especially of larger islands, another model would have proved a better fit. However, Connor and McCoy did not find this so in the data sets they studied: "Neither numbers, or orders of magnitude of area. . . . . . nor the particular orders of magnitude. . . . . . covered indicate which model should be the best fit", but they did make the point that to detect curves that are sigmoidal one should sample as wide a range of areas as possible, presumably of islands with similar climates lying within the same biogeographical region, if possible.

*The species-distance relationship*

Although in most instances (Table 3) the expected negative correlations apply between the number of species on an island and its distance from the supposed source (North, South and Stewart Island), none approaches significance and the values of r suggest that distribution of plants has been even less affected by distance than has that of insects. However, the range of distances is small-much less than those involved in many, if not most, studies of this kind; and it may well be that some species are not propagules or descendants of propagules but relicts of a once more widely distributed biota which have subsequently been transformed into insular species by rising sea levels.

In this relationship, in which none of the models

provide a satisfactory fit to the data, to term the log species-distance model the best would perhaps be inappropriate.

*The species-altitude relationship*

As can be seen from Table 4, the only significant value of r results from the use of the log/log model involving plants. However, if the influence of area is accounted for by partial correlation, then r (4 d.f.) = 0.591, which is not significant.\*

Though there is only one instance of a significant correlation in Tables 3 and 4, the results as found are published in response to Connor and McCoy's plea: "We especiaIIy encourage the publication of non-significant correlation coefficients. . . . . . values that now are probably eliminated by the review process, by an author's disbelief in his own results or the thought that they are uninteresting. Such examples are as informative about species-area relationships

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\* Although not part of the theme of this particular paper, multiple regression was used to assess the results, in their various combinations, of adding altitude and distance to area in regressions involving (i) the number of species of insects as a whole and (ii) the species of vascular plants. The untransformed data were used throughout. With two exceptions the result was to *decrease* the percentage of variance accounted for by the regressions. The two exceptions involved the insects: With distance added to area the variance accounted for rose from 74.4% to 80.9% and with altitude and distance added to area the variance accounted for was increased from 74.4% to 85.6%.

TABLE 3. *Analysis of the number of species vs distance from source for three insect orders and vascular plants on outlying islands of New Zealand, using the models discussed by Connor and McCoy.* (1979).

| | | MODEL TESTED | | | |
|---|---|---|---|---|---|
| | | Spp./ dist. | Spp./ log dist. | Log spp./ dist. | Log spp./ log dist. |
| Lepidoptera | r | -0.128 | 0.058 | -0.456 | -0.216 |
| | v.a.f. | -* | - | 5.0 | - |
| Diptera | r | -0.516 | -0.324 | -0.523 | 0.394 |
| | v.a.f. | 11.9 | - | 12.8 | - |
| Coleoptera | r | -0.240 | 0.073 | -0.507 | 0.346 |
| | v.a.f. | - | - | 10.9 | - |
| All the above | r | -0.339 | -0.137 | -0.481 | -0.319 |
| | v.a.f. | - | - | 7.7 | - |
| Plants | r | -0.050 | 0.144 | -0.037 | 0.003 |
| | v.a.f. | - | - | | |

* Residual variance exceeds variance of Y -variate.
$p = 0.05$ $r = 0.754$; $p = 0.01$ $r = 0.874$.

TABLE 4. *Analysis of the number of species vs altitude of islands for three insect orders and vascular plants on outlying islands of New Zealand, using the models discussed by Connor and McCoy* (1979).

| | | MODEL TESTED | | | |
|---|---|---|---|---|---|
| | | Spp./ alt. | Spp./ log alt. | Log spp./ Alt. | Log spp./ log alt. |
| Lepidoptera | r | 0.184 | 0.246 | 0.395 | 0.416 |
| | v.a.f. | -* | - | - | 0.7 |
| Diptera | r | 0.706 | 0.640 | 0.654 | 0.681 |
| | v.a.f. | 39.9 | 29.1 | 31.1 | 35.6 |
| Coleoptera | r | 0.188 | 0.250 | 0.398 | 0.449 |
| | v.a.f. | - | - | - | 4.2 |
| All the above | r | 0.410 | 0.429 | 0.510 | 0.558 |
| | v.a.f. | 0.2 | 2.0 | 11.2 | 17.3 |
| Plants | r | 0.332 | 0.390 | 0.707 | 0.847 |
| | v.a.f. | - | - | 40.0 | 66.0 |

* Residual variance exceeds variance of Y - variate.
$p = 0.05$ $r = 0.754$; $p = 0.01$ $r = 0.874$.

as are significant positive correlations, if not more so."

*The plant-insect relationship*

Though significant correlation is no proof of causation, that between the number of vascular plants and the species of lepidoptera + diptera + coleoptera (r = 0.937) is interesting because it seems reasonable to assume that there is some dependence of the insects upon the plants. Table 5 shows that, with one exception, the untransformed data again yield the best results; and comparison of this table with Table 2 shows that, using the best models in each instance, the number of species of vascular plants on an island is a better guide to the number of species of insects than is area. However, when, by using partial correlation, the common influence of area is removed from the plant-insect regression, its value of r (4 d.f.) is reduced from 0.937 to 0.660, which is not significant.

My findings support the warning given by Connor and McCoy: "The rationale for fitting the power function to all species-area data without testing the fit of other models appears to be a profound and perhaps unwarranted confidence that the species in question demonstrate a log-normal relative abun-

TABLE 5. *Analysis of the number of vascular plants vs number of species of insects for three insect orders on outlying islands of New Zealand, using tlte models discussed by Connor and McCoy* (1979).

| | | Plants / insects | MODEL TESTED | | |
| | | | Plants/ log insects | Log plants / insects | Log plants/ log insects |
|---|---|---|---|---|---|
| Lepidoptera | r | 0.985 | 0.858 | 0.600 | 0.685 |
| | v.a.f. | 96.4* | 68.3 | 23.2 | 36.3 |
| Diptera | r | 0.602 | 0.642 | 0.657 | 0.824 |
| | v.a.f. | 23.5 | 29.5 | 31.8 | 61.4 |
| Coleoptera | r | 0.966 | 0.839 | 0.617 | 0.750 |
| | v.a.f. | 92.1 | 64.4 | 25.7 | 47.5 |
| All the above | r | 0.937 | 0.812 | 0.696 | 0.808 |
| | v.a.f. | 85.3 | 59.1 | 38.1 | 58.3 |

\* % Variance accounted for by the regression; as calculated by the GEN-STAT program.

$p = 0.05$ $r = 0.754$; $p = 0.01$ $r = 0.874$.

TABLE 6. *The mean number of species/genus of insects (lepidoptera + diptera + coleoptera) and vascular plants in relation to the area of outlying islands of New Zealand. The "best fit" is that found by using the models discussed by Connor and* McCoy (1979). *(Bounty Islands support no vascular plants).*

| | | S/G RATIO | |
| | Area ($km^2$) | Insects | Plants |
|---|---|---|---|
| Chathams | 965 | 1.42 | 1.99 |
| Bountys | 1.3 | 1.00 | |
| Snares | 2.8 | 1.13 | 1.13 |
| Antipodes | 21 | 1.16 | 1.40 |
| Aucklands | 612 | 1.53 | 1.93 |
| Campbell | 114 | 1.43 | 1.78 |
| Macquarie | 118 | 1.25 | 1.17 |

*Best fit*
r(log area/log insects)  = 0.927, $p < 0.01$
r(log area/plants)  = 0.865, $p < 0.05$

dance distribution. . . . . . The inference that a significant fit necessarily implies an underlying log-normal distribution is . . . . . . ill founded. Clearly, a more reasonable course is to search out the model giving the best statistical fit." Finding the best fit is merely a matter of trial and error, though why there should be such unpredictability is not understood. Incompleteness or inaccuracy of data must play some part, and Connor and McCoy suggest that the sampling of a wide range of areas is necessary if a consistently best model is to be found. For the islands dealt with in this paper, the model using untransformed data proved best for the species-area and plant-insect relationships.

For the species-distance relationship there is no "best"–in the sense of "satisfactory"-model because of the poor fit between all models and the data (there are no statistically-significant values for any of the correlation coefficients). The same applies to the insects in the species-altitude relationship, but not to the vascular plants where there is a best model-that of the power (or log/log) function.

Since the power function model has become so much a part of the MacArthur and Wilson theory, any corroboration of Connor and McCoy's demonstration that it may not be the best of the four alternative models, even in a majority of instances, is worth drawing attention to. Connor and McCoy's paper plus two other searching criticisms of the equilibrium theory-Simberloff's (1976) and Gilbert's (1980)--clearly suggest, to use Gilbert's words, that the theory remains insufficiently validated to permit its widespread application to many problems of biogeography, ecology and nature conservation.

*The species / genus-area relationship*

If one assumes that the ecological diversity of islands generally decreases as area decreases and that congeneric species are more alike in ecological requirements than those belonging to different genera, then the likelihood of competition between congeners should increase as island area decreases, so leading to exclusions and the approach of the species/genus ratio to unity. Thus, S/G ratios should show positive correlation with island area (and with the number of resident species too, since N is also positively correlated with area). Table 6 shows that the expected correlation between area and S/G ratios exists

TABLE 7. *Species / genus ratios of land birds on islands, from Simberloff (1970). Column A: the number of islands for which the actual* S / G *ratio was* greater than *the estimated; Column B: the number of islands for which the actual S / G ratio was* **less than** *the estimated.*

| No. of species on island | Table 1 | | Table 1 modified | | Table 5 | |
|---|---|---|---|---|---|---|
| | A | B | A | B | A | B |
| 1-5 | 0 | 6* | 0 | 6* | 0 | 5 |
| 6-10 | 5 | 16 | 10 | 11 | 5 | 5 |
| 11-15 | 4 | 12* | 11 | S | 5 | 3 |
| 16-20 | 7 | 7 | 11 | 3 | 4 | 0 |
| 21-25 | 7 | S | 7 | S | 3 | 4 |
| Sub-totals | 23 | 46 | 39 | 30 | 17 | 17 |
| 26- 30 | 13 | 1 | 13 | 1 | 8 | 1 |
| > 31 | 27 | 6 | 27 | 6 | 17 | 2 |
| Sub-totals | 40 | 7 | 40 | 7 | 25 | 3 |

* Includes one instance of S/G (act.) = S/G (estimated)

The data in this table summarize (i) Simberloff's Table 1, sections 1-13 inclusive; (ii) that table modified by the replacement of its section 11 by Simberloff's Table 2; and (iii) his Table 5, which is his Table 1 with monotypic source species deleted.

for the islands dealt with in this paper. Is one then justified in joining with those, e.g. Grant (1966), who have interpreted such correlations as evidence for competitive exclusion being an important factor in determining biogeographical distributions on islands? Simberloff (1970), by showing that on purely mathematical grounds S / G ratios are, in any event, directly dependent on N (a fact which is by no means immediately self-evident) has discredited such an interpretation. But even accepting that S / G ratios should be lower if competitive exclusion is occurring, than they would be if islands' species complements were random subsets of the source pool, Simberloff found instead, from the large amount of island data analysed, that they were generally higher. This clear tendency for there to be be more congeneric species than expected he ascribed to species belonging to the same genus having similar ecological requirements and abilities to disperse; thus, in this context, effectively standing Gause's venerable hypothesis on its head. Though SimberlotI's test is persuasive, competitive exclusion is so widely accepted as axiomatic that one cannot help but feel that his analyses emphasise a paradox still to be fully resolved statistically.

One point he did not pick up in his analyses will be discussed here since it may prove to be significant when more data become available-at least locally-on the taxonomic composition of islands so small or ecologically simple that they support only a few species (as, for example, the Bountys-see below). Using his data on land birds and taking account only of whether the S / G ratio found on each island is greater or less than the calculated value, let us see how the relationship of S/G (actual) to S/G (estimated) is distributed according to the number of species found. (Simberloff obtained the estimated S / G ratio by taking from the presumed source pool 100 random samples, each of N species-the number actually occurring on the island-and calculating the mean of the 100 S / G values so generated). The data given in Table 7 summarize (a) Simberloffês Table 1, section 1-13 inclusive; (b) that table modified by the replacement of its section 11 by Simberloff's Table 2 (see below); and (c) his Table 5, which is Table 1 with monotypic source species removed.

It is evident from all three sets of figures that only when islands are, presumably, large or ecologically diverse enough to support more than about 25 species is there the clear preponderance that Simberloff emphasizes of actual S / G values which are greater than the calculated and hence more congeneric species present than would be expected from random colonization; whereas, on islands supporting 25 species or less, the process of colonization seems to be a random one. The figures for his *amended* Table 1 are not so unequivocal in this regard. They have been obtained by replacing the original section 11 in which the estimated S / G values depend on the assumption that Shetland Mainland is the source of

TABLE 8. *Insect fauna of the Bounty Islands*

| | | |
|---|---|---|
| ORTHOPTERA | | |
|   Rhaphidophoridae | : | *Ischyroplectron\* isolatum* (Hutton) |
| HYMENOPTERA | | |
|   Diapriidae | : | *Antarctopria diomedeae\** Early |
|   Pteromalidae | : | gen. et sp. indet. |
| DIPTERA | | |
|   Chironomidae | : | gen. et sp. indet. |
|   Tipulidae | : | gen. et sp. indet. |
|   Psychodidae | : | *Psychoda acutipennis* Tonnoir |
|   Dolichopodidae | : | *Aphrosylopsis lineatus* Lamb |
|   Canaceidae | : | *Macrocanae littorea* (Hutton) |
|   Ephydridae | : | *Neoscatella* sp. |
|   Sphaeroceridae | : | *Leptocera (Thoracochaeta)* sp. |
| COLEOPTERA | | |
|   Carabidae | : | *Bountya\* insularis* Townsend |
|   Tenebrionidae | : | *Pseudohelops liberalis* Watt |
|   Hydrophilidae | : | *Thomosis guanicola* Broun |
| LEPIDOPTERA | | |
|   Tineidae | : | *Proterodesma (Antipodesma) turbotti* (Salmon & Bradley) |
|   Psychidae | : | *Reductoderces* sp. |

\* Endemic at this level

the Shetland avifauna, (and in which only three of the 24 islands have an actual S/G ratio greater than the estimated), with his Table 2 in which he makes the apparently preferred assumption that Britain has been the source instead. (Now 17 of the 24 islands have actual S/G ratios greater than the estimated).

Simberloff's vascular plant data present a different situation: only three of 62 islands have actual S/G ratios equal to or less than the estimated values and none of these islands are among the five which support less than 100 species. (In his analysis of the plant data, Simberloff accepts Shetland Mainland and *not* Britain as being the source of the rest of the Shetlands flora-an unexplained inconsistency).

A similar analysis involving the islands treated in this paper is not, at present, feasible because of the lack of availability of the necessary data for the approximately 4500 indigenous species of coleoptera, 2000 diptera, 1500 lepidoptera and 2000 vascular plants. In any event, with so few islands and so limited a range of values of N, the analysis would be unlikely to prove a profitable one. But in the general context of competitive exclusion, the known insect fauna of the Bounty Islands is worth describing. There are 15 species; these belong to 15 genera which, in turn, belong to 15 families (Table 8). Apart from the lepidoptera, coleoptera and diptera there are two species of hymenoptera (J. W. Early, pers. comm.)–one of which is parasitic-and a flightless orthopteran.

There are two endemic genera and an endemic species; the remaining 12 species probably occur either on the Antipodes or The Snares, or both. (There are also two species of spiders, each belonging to a different family). To what extent such a distribution of taxa is the result of chance or adaptability of the few species to an environment extremely limited in both habitats and niches is an interesting conjecture; competitive exclusion does not seem a likely explanation in this instance–one would not expect it to extend to the family level. The Bounty situation suggests that species lists of islands similar in ecological simplicity should be examined more closely than a mere species number-area study, similar to Simberloff's (1970), would usually involve. Such examination might yield important information about the factors determining the complement of taxa on islands which support only a few species; and this information may, in turn, throw more light on the general species-area problem.

In a more recent paper, Simberloff (1978) points out that most of the evidence cited in support of the operation of competitive exclusion is circumstantial and of the *post hoc* kind. (And one could add that although congeneric species may be more alike than non-congenerics it is probably unjustifiable to con-

clude that they will always seriously compete with each other on islands, whether they arrive together or separated by some considerable time. Ecologically, they cannot be assumed to be always that similar, nor can the new environment be assumed to be always sufficiently limited in habitats and niches). Simberloff continues "one must recognise that the tendency toward higher similarity generated by good colonizers could swamp a real but lesser tendency toward lower similarity generated by competition. This is an inherent weakness of distributional data which are the resultants of several underlying forces". As a result of his analysis of the distributions dealt with in his paper he concluded that a purely stochastic model of colonization which rests only on properties of individual species came close to accord with some plant and insect data and could, in any event, be used for testing whether other phenomena need to be assumed.

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ADDED IN PROOF

Two vigorous counter attacks supported by sophisticated statistical fire-power have been made on Connor, McCoy and Simberloff by Sugihara (1981) and Diamond and Gilpin (1982). Sugihara's target is Connor and McCoy's best-fit test and their interpretation of parameter z; Diamond and Gilpin's is Simberloff's and McCoy's use of "null" (sic) hypotheses to discredit the role played by interspecific competition in determining the structure of species communities on islands.

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