

INTERSPECIFIC COMPETITION, ISLAND BIOGEOGRAPHY AND NULL HYPOTHESES

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We conducted a field study of some of Darwin's Finches (*Geospiza* species) in order to assess the relative importance of interspecific competition and habitat features in determining the observed biogeographic, ecological and morphological characteristics of these species (Abbott et al., 1977). Strong et al. (1979) have criticized one of our methods and have reanalyzed a small portion of our data. They employed stochastic models to generate expected beak size differences between sympatric species, and then compared expected with observed differences. Finding a generally close correspondence between expected and observed differences, they concluded that random processes are sufficient to account for the observations, and that therefore there is no need to invoke deterministic processes such as competition as we had done. Strong et al. (1979) obtained the same results and drew the same conclusion from analyses of beak size differences among birds on the Tres Mariás islands of Mexico and the Channel islands of California. Simberloff and his associates have also drawn the same conclusion from a series of other analyses performed in like manner (Connor and Simberloff, 1978; Simberloff, 1978).

We take issue with the procedures Strong et al. (1979) have used in their analyses and with the way in which our statements and interpretations have been represented. We identify five problems in their analyses and five sources of confusion in the interpretation of results. We find no evidence in their analyses or arguments to change our previous conclusion that interspecific competition has played a role in the adaptive radiation of

Darwin's Finches. Finally, we draw attention to some unsolved problems in biogeography, concerning principally the separation of potentially conflicting effects of different processes such as dispersal and competition.

Why Their Methods are Unsatisfactory

Strong et al. (1979) generated expected ratios of beak sizes among birds on the California Channel islands, the Tres Mariás islands and the Galápagos. For the first two groups of islands they used a computer to draw randomly the observed number of species on each island from within families of birds on the adjacent mainland. They repeated the exercise 100 times to obtain an estimate of sampling error. For the Galápagos they chose species at random, then a population from one of the islands at random for each of the species already chosen, until the number of species populations matched the observed ones on all of the major islands. Ratios were calculated separately from observed species combinations and randomly paired species, and then compared.

There are several problems with these procedures. In several ways the analyses tend to maximize the risk of making a Type II error, that is, favoring acceptance of the null hypothesis when it is false.

1. The first problem is that the choice of species within families is unfortunate. Species of birds in different genera are less likely to be in the same feeding group or guild than are species in the same genus, and hence are less likely in general to be in potential competition for food (exceptions are easy to conceive, and observe,

Grant, 1966). We know of no systematic study undertaken to test this assertion, but it is a view commonly held on the basis of observations and from the reasoning that the more closely related two species are the more they will have similar adaptive systems for locomotion, food gathering, breeding, etc. (e.g., Darwin, 1859; Hairston, 1964; Lack, 1965).

A simple illustration can be given with Darwin's Finches. Species in the genus *Geospiza* show strong similarities in feeding methods, locations and actual diet (Snodgrass, 1902; Lack, 1945, 1947; Bowman, 1961, 1963). Our study provided a quantitative confirmation of this similarity. Species in the genus *Camarhynchus* also show strong similarities in feeding methods, etc., but differ markedly from all *Geospiza* species on the one hand and from *Certhidea olivacea* on the other (references above). Pooling all species from these three genera, then choosing pairs at random to examine beak ratios, is a meaningless exercise as a test of competitive effects because there is no a priori reason to believe that unrelated species would compete, except under the most extreme view that diffuse competition noticeably affects all species in a community. We suggest that it may be worse than meaningless; it may obscure real competitive effects within genera by diluting the phenomenon to the point of disappearance. Caswell (1976), Colwell (1979) and Inger and Colwell (1977) have made a similar point.

Grant (1980) has shown with a multivariate analysis of beak dimensions that populations of sympatric pairs of *Geospiza* species are not a random sample of all possible paired populations of those species; observed pairs tend to differ more than randomly chosen pairs. Character displacement is a possible, but clearly not necessary or sufficient, explanation (Grant, 1979). In some of their analyses Strong et al. (1980) used *Geospiza* and *Camarhynchus* species together, and found that observed sympatric assemblages of species (pairs, triplets, etc.) can be considered random samples. We suggest the differ-

ence in results stems from a difference in the species pool. We consider our species pool to be appropriate and theirs to be inappropriate.

This point is of general importance. Strong et al. (1979) could find no reason to reject the null hypothesis for the total Tres Mariás and Channel island data. Yet the beak sizes of members of the same feeding guild suggest that competition has influenced part of the structure of the Tres Mariás avian community (Grant, 1966).

The only biological justification for using the family level in treating the data that we can find is in Simberloff (1978, p. 714)—“Still more important than the low visibility of interspecific competition in obscuring its relationship to biogeographic distributions is the fact that putative competitors are rarely pairs of taxonomically [congeneric?] and morphologically similar species.” This claim is unsubstantiated, which should therefore serve as a stimulus for further research. An analytical justification is that the family level of analysis is less sensitive to specific taxa than is the genus level (Strong et al., 1979). Be that as it may, resorting to the family level of analysis runs the risk of throwing the baby out with the bath water; or, to be more correct, drowning the baby by using too large and deep a tub.

2. The second problem is in the choice of a mainland area for comparison with the island (Grant, 1966). Geographical variation in community membership and beak sizes of the members within the mainland region could influence the results of a random simulation of the process of island colonization.

In an earlier analysis of the species/genus ratio of island bird communities, Simberloff (1970) showed that observed ratios tended to be higher than those expected from the random sampling of mainland species, and certainly not lower as would be expected from an hypothesis of competition (Grant, 1966). With regard to the problem of correctly identifying the source pool of species on the mainland, he wrote, “A study currently in progress indicates there is little geographical variation in S/G

[species/genus] values for land birds, particularly when localities of similar latitude are compared" (Simberloff, 1970, p. 27). The source pool for the California Channel islands and Tres Mariás islands probably comes from areas more extensive longitudinally than latitudinally. One therefore wonders how errors of choosing the correct source pool might influence the results of species/genus and beak difference analyses using the stochastic model approach. Given this uncertainty, and for maximum biological realism, the safest procedure is to use the species in an adjacent mainland area equal in size to the islands (Grant, 1966; Abbott, 1975), rather than all those in a whole country such as Mexico (Simberloff, 1970). The chances of detecting nonrandom colonization are greatly reduced by using excessively large mainland species pools when the mainland communities vary geographically in a systematic way.

3. In the original analyses Simberloff (1970) assumed equiprobability of dispersal among all species in the mainland pool, in order to obtain expected species/genus ratios on islands. This assumption seems unlikely to be true (Grant, 1970; Terborgh et al., 1978), as has been recently acknowledged, "Biologically this assumption implies that all species have equal dispersal and persistence abilities. In fact, species have different abilities to disperse and persist, and this assumption is therefore absurd" (Connor and Simberloff, 1978).

Our purpose here is to point out that until a biologically realistic stochastic model can be constructed, with allowance made for different dispersal abilities, the observed species/genus ratios and "community-wide" beak ratios of birds on islands cannot confidently be ascribed solely or predominantly to random processes. When equal weight is given to species with low or zero probability of dispersal and to species with high probability of dispersal, the analysis is tipped in favor of accepting a null, random, hypothesis. Simberloff (1978) has shown that the expected number of species shared by two

islands is strongly influenced by the equiprobability assumption. We suspect that other expected biogeographic, ecological and morphological properties of island populations are similarly affected. This is not intended to belittle the attempts to come to grips with a very complex problem; only to point out that the problem has not yet been solved, and the interim report is not convincing.

4. The fourth problem concerns the generation of expected beak size ratios for archipelago islands (e.g., Galápagos) when there is no identifiable mainland source area and species pool. The solution adopted by Strong et al. (1979), Connor and Simberloff (1978) and Simberloff (1978) in similar analyses, is to treat the archipelago as a universe from which individual islands are populated. Beak ratios are calculated (Strong et al., 1979) from randomly combined populations; then the results of repeated random pairings are compared with the actual data.

Our criticism here is that the two samples tested for similarity (the real data is one sample, and the set of randomly generated faunas is the other) are not independent. In fact, the real data for any given island are a subset of the randomized data. The statistical bias that this kind of nonindependence causes is not random; it consistently favors the acceptance of the null hypothesis, and hence maximizes the risk of making a type II error, since the two samples are artificially made more similar by the inclusion of the same data in each.

Presumably the justification for their procedure, following explicit statements in Connor and Simberloff (1978) and Simberloff (1978), is that the method of combining populations at random "does not uniquely determine" the observed ratios, "and so the tests are not circular" (Connor and Simberloff, 1978). If not circular they are at least elliptical, for all populations of the *Geospiza* species on the 15 islands they considered are sympatric with at least one other species, that is, all species populations enter the calculation of expected ratios and all provide the observed ratios

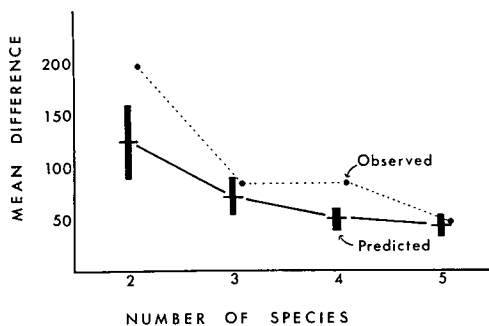


FIG. 1. The average difference between size neighbours in beak size and shape in relation to the number of species on an island. Differences are Mahalanobis D^2 values, calculated on the basis of beak depth, length and width for each pair of species (Grant, 1980). To generate the predicted curve, species were randomly combined in pairs, triplets, quartets and quintets, and arithmetic mean D^2 values (horizontal lines) and 95% confidence limits (vertical bars) were calculated from samples of 50. Data in Abbott et al. (1977) and Abbott et al. (unpubl.) were used in the calculation of the observed differences.

with which the expected ratios are compared. The calculation of dispersal abilities from observed frequency-of-occurrence distributions (Connor and Simberloff, 1978; Simberloff, 1978) is subject to the same criticism.

5. Their analysis of just the *Geospiza* data alone is the most similar to ours. They obtained a negative correlation between expected average minimum ratios and number of species, and concluded that "a negative correlation is expected from randomly assembled communities, so finding a negative correlation among real communities does not show character displacement" (Strong et al., 1979, p. 900). We agree that although a *competition* hypothesis predicts a negative correlation, it is also to be expected from a random (noncompetition) hypothesis. This is because a rank-ordered sample is like a broken stick—the more breaks (large sample) the smaller the pieces (ratios of adjacent bill sizes). The problem then is to distinguish between the two hypotheses.

The task is not easy because there are three objections to the construction of a simple random model with which to com-

pare the data. First, as mentioned above, the random sampling assumes equal dispersal abilities for all populations of all species; this is unlikely to be even approximately correct. Second, observed and expected ratios are not independent. Third, there is a tacit assumption that the birds have fixed properties, that is, no in situ evolution, for the pattern of beak ratios can be simulated simply by randomly combining existing populations without requiring further change in beak dimensions. A "no-evolution" assumption leaves hanging the question of why populations of the same species differ in beak size among islands in the first place, and why no two sympatric species differ by less than 15% in at least one beak dimension (Grant, 1975, 1980). Are we to attribute this complex pattern of variation to chance? Doubtless a stochastic model could be constructed which gives results approximating observed variation (cf. Raup and Gould, 1974), but would the assumptions be any more acceptable? In sum, the random model is patently unrealistic.

These difficulties are compounded by the test procedure used by Strong et al. (1979). They tested the distribution of observed minimum beak size ratios above and below the mean of the null community by a 2-tailed binomial test. This is not the most powerful test to use because it takes no account of the known magnitude of deviations of observed from expected values; the same criticism applies to some of their other analyses. Moreover a 1-tailed test is appropriate because unidirectional deviations from random expectation are predicted from a competition hypothesis. These are important points because from their Figure 1 it appears that the observed mean for every sample is greater than the null mean. This trend, if correct, is consistent with a hypothesis of competition.

We have performed a multivariate version of the Strong et al. analyses, and this has produced grounds for rejecting a random hypothesis and accepting a competition hypothesis (Fig. 1). Observed beak

ratios tend to be larger than those expected from randomly combined species. The three objections listed above apply to our analysis as much as to the analysis of Strong et al. Note, however, that statistical evidence partly favors a competition hypothesis despite a bias towards accepting the null (random) hypothesis. Without complete confidence in the method of analysis, we conclude that beak ratio data give evidence of competition among *Geospiza* species.

Strong et al. (1979) performed one further test with the *Geospiza* data. We suggested that competition may have stronger effects on islands with fewer species than on islands with many (Abbott et al., 1977). Strong et al. (1979, p. 901) reasoned from this that there should be "a tendency for islands with fewer species to fall farther above expected" [in the analysis discussed above] than those with more species. This was tested by comparing observed minus expected beak ratios with number of species per island. As expected from the competition hypothesis the sign of the correlation coefficient was negative in two analyses with *Geospiza* data (beak length and beak depth) but the correlations were not statistically significant. They concluded, "If character displacement does operate through minimum ratios of sympatric finches, this sort of community-wide analysis cannot detect it" (p. 901). We agree with the conclusion, but for a different reason. With only two degrees of freedom in each correlation analysis, a near-impossible demand is being made of the data.

Other Misrepresentations and Confusions

1. There is confusion over the term character displacement. As has been pointed out before (Grant, 1969), an enhanced character difference, such as a large difference in bill size between two sympatric species on an island, can be brought about by competition in two ways; by the elimination of intermediate-sized species (differential colonization, an ecological process) and by an evolutionary response of one or both species (character

displacement, an evolutionary process). Strong et al. (1979, p. 897) point out the distinction in their introduction, but then go on to use the term character displacement to include both processes. This is confusing because it is inconsistent with other specific definitions of character displacement as an evolutionary process (e.g., Grant 1972a).

Thus Strong et al. (1979, p. 899–900) wrote, "Abbott et al. (1977, p. 164, figure 12) have concluded character displacement to be common in *Geospiza*." Elsewhere we are represented as claiming "that there is greater character displacement on islands with fewer *Geospiza* species" (p. 900), "infer[ring] a version of community-wide character displacement among the Galápagos finches" (p. 908), and that we "assumed character displacement" (p. 909).

In fact, we claimed to have found evidence of *interspecific competition*. Our data did not allow us to choose between explanations involving the very different processes of differential colonization and character displacement (sensu Grant, 1972a). The choice can only be made where 'mainland' source populations and colonization routes are readily identifiable (Grant, 1969). Within the Galápagos archipelago it is rarely possible to trace out colonization routes with confidence (Grant, 1967). Bearing this in mind we drew a cautious conclusion about character displacement (sensu Grant, 1972a). "So by this indirect argument [see Abbott et al., 1977, p. 176, for details] we infer that some morphological and ecological character displacement probably occurred, either in the initial stages of differentiation or during the subsequent establishment of sympatry with the closest relative, although we cannot say in which particular cases."

In short, we claim that interspecific competition has occurred among Darwin's Finches, and that character displacement was the consequence in some unidentified instance.

2. "The assumption that insular coexistence begets greater sympatry than conti-

mental coexistence is of untested general validity, but it is common in the ecological literature (Abbott et al., 1977). We would suppose that geometrically congruent sympatry among species sometimes but not always occurs on islands, and that it is less frequent on mainlands" (Strong et al., 1979, p. 909).

We neither referred to the assumption in other work nor made it in our own as we were not concerned with making comparisons between islands and mainland. Regardless of how one defines "geometrically congruent sympatry," there is empirical evidence that most of Darwin's Ground Finches (*Geospiza* species) on the same island live in the same environment and encounter each other (Gifford, 1919; Lack, 1945, 1947; Bowman, 1961; Abbott et al., 1977): they coexist in sympatry.

3. "As an example of our reasoning, we disagree in principle with Abbott et al. (1977), who conclude that food supply and interspecific competition have jointly determined the patterns of evolution and species diversity of the Galápagos Finches. If their analyses of competition and habitat were adequate, only a portion of the evolution and ecology of the finches has been determined by these factors" (Strong et al., 1979, p. 910).

Since we did not say that the two factors *solely determined* the patterns, these remarks are as misleading as they are unnecessary. Some investigators set up a problem in such a way that all variation in a phenomenon can be attributed to two or three factors and to no others (e.g., Terborgh, 1971). We did not adopt this circumscribed approach. In the Introduction we stated, "We report results of field studies undertaken to investigate *some factors* responsible for inter-island differences in ground-finch morphology and ecology" (p. 152; italics added). The rest of the Introduction makes it clear why these particular factors were chosen for detailed analysis. We also made the necessary statement that many factors affect complex phenomena, for example, "Gaps [in the distribution of a species] such as these could result from chance extinctions,

competitive exclusion by congeners, unsuitable structural habitat, absence or scarcity of preferred or suitable foods, or inability to cross to some islands sufficiently often or in large enough numbers (chance colonizations)" (p. 169; see also Grant, 1966).

The second sentence in the quotation from Strong et al. (1979) implies that our analyses were inadequate. We have already given reasons for considering ours adequate and theirs inadequate. Here we take the opportunity to point out that our conclusions rest on many more analyses than the one contested by Strong et al. (1979); these involved numbers and biomass of finches, diets in relation to beak morphology, morphology in relation to abundance, distributions and combinations of species on islands, habitat diversity and predation, all of which were used to test traditional null hypotheses.

4. In an earlier analysis, bill size differences between congeneric species of birds were found to be more frequently larger on the islands of West Indies than on the nearby mainland, to a statistically significant extent (Grant, 1968). Strong et al. (1979) were unable to duplicate these results, and found the trend to be present but not statistically significant. We in turn have been unable to duplicate the results of Strong et al. (1979). In view of the uncertainties about the most appropriate mainland source pool with which to compare the islands, we tried different areas of mainland (e.g., North and Central America, Central America alone). The results were the same as in the original analysis; we see no reason to alter the original conclusion. Since the original data are published in Schoener (1965), it should be possible for someone neutral to the argument to settle it.

5. "Although character convergence is predicted from some models of community integration (Schoener, 1969; Cody, 1973), we agree with Hespeneide (1973) that convergence and displacement are quite opposite phenomena. The fact that both are predicted from competition theory might render the theory a catholicon, es-

pecially if the theory cannot predict which should occur in specific instances" (Strong et al., 1979, p. 908).

Two points may be made in reply to this. The first is that the equilibrium theory of island biogeography itself might similarly be viewed as a "catholicon" (cf. Abbott and Grant, 1976), as it encompasses both equilibrium states and nonequilibrium states which will presently or eventually lead to an equilibrium (MacArthur and Wilson, 1967). Despite this disadvantage, it has led to much productive research on mechanisms and processes because its elements can be tested, and it has not yet been replaced by a more obviously falsifiable theory.

The second point is that there is a logic which connects divergence and convergence. Both are predicted from competition theory. They are alternative solutions to basically the same competitive problem in different ecological circumstances. Moreover the most comprehensive set of models specifies the different conditions under which each result is expected (Wilson, 1975). Furthermore, Wilson (1975) has pointed out that one particular observed convergence, involving copepods studied by Rigler and Langford (1967), conforms to the model. This is not to say that all convergences and divergences are brought about by competition (Grant, 1972a). A judgement has to be made on the possible role of competition, on the basis of evidence from geographical variation, feeding ecology, etc. Nor does this say that divergence and convergence are equally likely to be brought about by competition; divergence seems generally the more likely (see Grant, 1975; Wilson, 1975).

DISCUSSION

One of the main themes in the papers by Connor and Simberloff (1978), Simberloff (1976, 1978) and Strong et al. (1979) is that there is a need for testing hypotheses involving competition or any other deterministic process against appropriate null hypotheses. Their attitude is summarized, "We propose another possibility

with logical primacy over other hypotheses, that other hypotheses must first be tested against, but that is rarely considered at all by ecologists. This is the null hypothesis that community characteristics are apparently random" (Strong et al., 1979, p. 910).

The logical primacy of randomness is debatable. Where different causal factors are implicated in the determination of complex phenomena like community structure, it is just as valid to test contrasting deterministic explanations against each other as it is to test each one against a random hypothesis. However, regardless of logical primacy, the use of non-interactive models in community studies holds much promise (e.g., see Caswell, 1976; Hubbell, 1979), in two respects. Such models should help to clarify the importance of randomness itself, while at the same time they are likely to stimulate more rigor in attempts to demonstrate the operation of causal factors, as has happened in population genetics through the neutralist-selectionist debate. To elaborate the first point, randomness in the null hypothesis used by Strong et al. (1979) is only partial, for the components of the hypothesis—species and their attributes—have been supplied by nature; it is their relations which are random. So the important question is, how much have random processes shaped communities?

If the history of studies of population cycles are a guide to what we might anticipate in community studies, the introduction of random models (cf. Cole, 1951, 1954) will take the mystique out of macroscopic phenomena, such as log-normal distributions of species abundances, and force critical attention upon the mechanisms and deterministic processes that produce repeated, biologically interpretable, patterns and events (Christian and Davis, 1964; Chitty, 1967; Krebs and Myers, 1974; Lidicker, 1975). Another lesson which may be learned from population studies is that random patterns are no guarantee of random causes, for Hassell et al. (1976) have shown that deterministic models of single populations can yield ran-

dom fluctuations of numbers in time (see also Gilpin, 1975).

Our criticisms have not been directed at the need for appropriate null hypotheses, with which we firmly agree, but at the use of a particular randomization procedure to construct these null hypotheses. The artificiality of the random 'scrambling' model and in some instances its dependence upon the data that are used to test it, reduce its acceptability.

Another problem in biogeography and evolutionary biology which is illustrated by this debate is the need for critical tests that will allow confident rejection, as opposed to nonacceptance, of a particular hypothesis. For example, consider the hypothesis that the low species/genus ratio of birds on islands is determined in part by interspecific competition (Grant, 1966). Simberloff (1970) and Abbott (1975) have shown that observed ratios are actually higher than expected from an hypothesis of random sampling of mainland species. On the surface this would appear to be not just nonacceptance of the competition hypothesis but a clear rejection of it, because departures of observed from expected are in the opposite direction from those predicted by the competition hypothesis. Aside from the difficulties with the random model discussed earlier, there is a hidden complication. Species within a genus may have similar propensities to disperse and colonize islands. If these are greater within some genera than others, as seems likely to us and to Simberloff (1970), the species/genus ratio on islands could be in equilibrium between two opposing processes—differential dispersal among genera, tending to elevate the ratio, and intragenetic competitive exclusion, tending to lower it. If so, the observed higher-than-expected ratio provides no evidence for a process, competition, which has actually operated, because another process, differential dispersal, has been of over-riding importance. Therefore the competition hypothesis has not been adequately tested and rejected by comparing species/genus ratios on islands and mainland.

Instead, the results of competition may be manifested by which particular species in a genus are present on an island, and their bill sizes and associated characteristics. These manifestations were shown to be consistent with an hypothesis of competition in a study of the birds of the Tres Mariás islands (Grant, 1965, 1966). Sixteen congeneric pairs of species could occur on these islands, as deduced from the pattern of occurrence of species among genera on the mainland and the occurrence of genera on the islands. But only two pairs actually occur on the islands. These are the second and fourth most dissimilar pairs in bill length. The occurrence of two such dissimilar pairs by chance seems unlikely, although attaching probabilities to so few occurrences is difficult. However, an independent test of the competition hypothesis was made with more extensive data from the West Indies, and it gave a similar result; the competition hypothesis was supported by the way in which a null hypothesis was rejected (Grant, 1969).

Where there is little or no scope for differential dispersal among genera we would expect competitive effects to predominate. This may be the case on the Galápagos. Thirteen of 15 islands have lower species/genus ratios of birds than expected by a random sampling procedure (Connor and Simberloff, 1978). The authors did not test the null hypothesis that as many islands have higher ratios than expected as have lower ratios than expected. It is rejected by a 1-tailed Sign test ($P = .011$). There are other interpretations of this result (Strong et al., 1979; see also Connor and Simberloff, 1978), but the point is that the competition hypothesis cannot be ruled out.

Such conflicting processes complicate analyses of biogeographic patterns (Simberloff, 1978). While the refinement of stochastic models may help to resolve these complications, we propose that detailed ecological studies hold out better hope, particularly if experimental and if directed towards specific questions of competition and dispersal (Simberloff, 1969, 1976;

Simberloff and Wilson, 1969; Grant, 1972b).

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SUMMARY

Some of the evidence for interspecific competition among Darwin's Finches (Abbott et al., 1977) has been challenged by Strong et al. (1979). These authors were able to predict the degree of morphological differences actually observed among the finch species from stochastic models. They concluded it is unnecessary to invoke deterministic processes such as competition. We argue that their methods of analysis are seriously flawed by a lack of realism and by biases that tend to favor acceptance of the null hypothesis, hence their conclusions are unacceptable:

- a) All species within a family were compared, even though some are so different ecologically that competition between them is, a priori, extremely unlikely. An analysis by genera as was done for *Geospiza*, or by feeding guild, is more meaningful.
- b) All populations of all species were assumed to have equal dispersal abilities and equal chances of reaching all islands in the archipelago; this is extremely unlikely to be even approximately true.
- c) A tacit assumption of no-evolution in the construction of random models leaves hanging the question of why populations of the same species differ in beak morphology among islands, and why no two congeneric, sympatric, species differ by less than 15% in at least one beak dimension.
- d) Expected and observed ratios of beak size were not independent.

The first two objections also apply to predictions of island bird properties from a knowledge of mainland birds. Some confusions over the nature of character displacement, the degree of sympatry on islands and the relative importance of interspecific competition are dealt with. Current problems in biogeography in need of attention are (1) separating the potentially conflicting effects of different processes, such as competition and dispersal, and (2) devising tests which permit clear rejection, as opposed to nonacceptance, of an hypothesis. We conclude that stochastic models may be a useful tool in hypothesis testing in biogeography, but until they can be made realistic their usefulness will be severely limited.

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