EPILOGUE

If your head is wax don't walk in the sun.
—Benjamin Franklin, *Poor Richard's Almanac*

In the preceding chapters, we discussed the history and application of null models in ecology. It should be clear to readers that we view null models as an integral part of the hypothetico-deductive method in science (Platt 1964, Connor and Simberloff 1986) and believe they have had a positive impact on community ecology. Nevertheless, null models have their limitations and can be subject to much abuse if certain aspects of quality control are neglected. Although it is more difficult to create than to criticize, our objective in this Epilogue is to point out some problems in the construction of null models that have been somewhat neglected in the literature.

CONSTRUCTION OF SOURCE POOLS

Although considerable attention has been focused on randomization algorithms in null models (see Chapter 7), the construction of species source pools and the underlying quality of the data have received less scrutiny. The species source pool for an island should include all species that have a *reasonable* probability of occurring on that island. Usually, the more isolated the island or archipelago, the fewer of its resident species are shared with other islands or mainland areas. If the fauna has undergone in situ speciation or differentiation, it may be even more difficult to designate an appropriate source pool. For reasons of convenience and tradition, source pools are often taken as the collection of all species in the archipelago (e.g., Strong et al. 1979), even when there is clearly the potential for colonization from adjacent mainland areas (e.g., Gotelli and Abele 1982). However, the source pool for two islands in an archipelago will rarely be identical, and source pool designation can have a strong effect on the outcome of null model tests (Graves and Gotelli 1983; Schoener 1988a).

A good example of variation in source pool construction can be found in a controversial series of analyses of the avifauna of the four Tres Marias Islands, which lie about 100 km off the Pacific coast of Mexico. The initial paper in the series was Grant's (1966) investigation of character displacement in ecologically similar species of Tres Marias birds. To determine whether bill sizes of island birds were unusual, Grant (1966:452) compared them with a pool of species from "an equivalent part of the mainland (same area and range of altitude, similar habitats, etc.)." He concluded that character displacement did occur among congeneric species on the islands.

In a study of species/genus (*S/G*) ratios of birds of the same islands, Simberloff (1970) included all species that occurred within 300 miles, excluding Baja California, in the source pool. A decade later, Strong et al. (1979:898) included species in the Tres Marias source pool "with habitat requirements and distributions such that they would likely inhabit the islands, and exclude species with obviously special habitat requirements that are not satisfied by the islands," that occurred in Nayarit and adjacent states. Grant and Abbott (1980) criticized Simberloff's (1970) source pool as being so large that nonrandom colonization might not have been detected had it occurred. Hendrickson (1981) went on to suggest a source pool of intermediate size, restricted to species from the nine avian families that occur on the islands that are resident at low elevations (900 m and below) in the states of Nayarit, Sinaloa, and Jalisco.

Simberloff (1984) followed these suggestions and reanalyzed the expected number of congeners on the islands using three mainland source pools, those of Grant (1966), Simberloff (1970), and Hendrickson (1981). He found that island generic compositions did not differ from random expectations regardless of the source pool used in calculations. Testing multiple source pools was an important innovation in null model analyses. Although the results did not differ in this case, Schoener (1988a) and, to a lesser extent, Graves and Gotelli (1983) both found that null model results were sensitive to source pool designation.

The Tres Marias source pools discussed above could be improved in several ways. The four islands parallel the coastline and span some 80 km. They vary considerably in elevation, area, and habitat (Nelson 1899). Yet, all the previous studies (Grant 1966: Simberloff 1970; Strong et al. 1979; Grant and Abbott 1980; Hendrickson 1981; Simberloff 1984) treated the four islands as a unit with identical source pools. If the distance between the source pool and the islands affects colonization probabilities (MacArthur and Wilson 1967), then source pools for widely separated islands are not identical. This is especially true for species-rich areas where many terminal range boundaries occur on the adjacent mainland.

In other words, species that occur within an arbitrary distance of one island [300 miles in Simberloff's (1970) analysis] may be outside that limit for another island in the same archipelago. This problem is magnified for large archipelagoes that are colonized from several mainland regions (e.g., the West Indies). Biogeographers continue to rely heavily on faunal lists from irregularly shaped geopolitical units. These data are easy to gather, but political states are rarely comparable on the basis of area and shape. Standardization of source pool areas can be achieved in several ways. We recommend that the source pool area for an island be delimited by a circle with a standardized radius (Graves and Gotelli 1983; see cover).

Habitat availability is of primary importance in determining what subset of the mainland avifauna could successfully colonize and persist on an island. The difference between the "total" source pool and the "habitat" pool can be substantial. The "total" pool consists of all mainland and island species within a geometrically standardized area, while the "habitat" pool (a subset of the total pool) includes only those species that breed in the spectrum of habitats present on the island.

We assume that source pool species that occur only in habitats not found on an island would not be expected to occur on it. This is not the same as saying that if a species does not occur on the island, one wouldn't expect it to. There are certain species that for all intents and purposes, have an infinitesimal probability of colonizing an island lacking its preferred habitat. For example, a habitat specialist of timberline coniferous forests of the Sierra Madre is unlikely to colonize the relatively low and dry Tres Marias Islands.

Both the total pool and the habitat pool are viewed from the frame of reference of the island, but the numerical difference between them for a habitat-depauperate island adjacent to a diverse mainland may be severalfold (Graves and Gotelli 1983). This technique allows one to standardize island-mainland comparisons for islands that differ greatly in habitat diversity. The determination of source pool status must be made on a case-by-case basis for each species and each island. As the type, area, and quality of habitats varies among islands, so does the potential source pool of colonizing species. Therefore, unless it can be demonstrated that the habitat characteristics of two islands are indistinguishable, their source pools must be independently derived. Although Grant (1966) and others acknowledged the role of habitat by restricting source pools to species from certain elevational zones, they still considered the source pools of all four islands to be identical.

What is the appropriate size of the Tres Marias source pool for null model tests of S/G ratios and size ratios? The radius of a circular source pool centered on the island should be large enough to incorporate a substantial enough area of

the mainland to support the full range of habitats found on the focal island. For land-bridge islands within 100 km of the mainland, we have found that a source pool of radius 300 km is generally sufficient to achieve this objective (Graves and Gotelli 1983; Gotelli and Graves 1990).

For the Tres Marias avifauna, source pool radii of 400 or more kilometers include a larger set of potentially colonizing species, but also include species with little chance of colonizing a distant island because of small populations and restricted geographic ranges (Grant and Abbott 1980; Graves and Gotelli 1983). In any event, source pools cannot be adequately designated without detailed knowledge of the habitat characteristics of the island and mainland as well as the ecological requirements of source pool species. The effect of source pool size on null model results should be checked whenever possible (see Simberloff 1984). For instance, the inclusion of additional congeners or guild members from an enlarged source pool may change the results of a null model analysis from significant to nonsignificant, or vice versa.

Finally, we recommend that source pool methodology be discussed in detail in null model papers. If the entire species pool cannot be published in an appendix, then it should be submitted to a data bank for future reference. Situations such as the conflict over unpublished data for the Bismarck Archipelago (Connor and Simberloff 1979) and the Tres Marias Islands (Hendrickson 1981) should not be permitted by editorial boards of technical journals. In both of these cases, the cited authors were unable to obtain species lists from the authors of earlier publications (Diamond 1975, and Strong et al. 1979, respectively).

SPECIES TAXONOMY

Taxonomy has a considerable, but largely ignored, importance in null models. Even for relatively well-known groups of plants and animals, differences in taxonomy can affect the number of species in island biotas and source pools. For higher vertebrates, the recent surge toward usage of the "phylogenetic" species concept (Cracraft 1983), as opposed to the more widely recognized "biological" species concept (Mayr 1963), has nearly doubled the number of recognized "species" in certain avian genera (cf. Morony et. al. 1975; Sibley and Monroe 1990). The development of source pools for null models of island colonization has been most successful for vertebrate communities, principally birds; invertebrates and plants of islands and mainland areas are more poorly known. Cryptic or undescribed species may also be common in certain taxonomic groups, especially in tropical regions, thwarting source pool construction.

Null models are usually based on data compiled from papers, books, and technical reports, while fewer are based on raw unpublished data. We encourage ecologists to collaborate with systematists and to deposit voucher specimens in a recognized systematic collection in order to ensure quality control and repeatability, should a subsequent analysis be desired. At the very least, the taxonomic authority or reference for species lists should be stated in the methods section of studies using null models.

SEXUAL DIMORPHISM AND GEOGRAPHIC VARIATION

Sexual dimorphism in body mass is often ignored in null models of character displacement. For example, Schoener (1984), in a worldwide study of size differences among sympatric bird-eating hawks, averaged the size of males and females to produce a single value for each species. Size averaging was performed to facilitate modeling, but it hardly duplicated the distribution of body sizes present in communities of raptorial birds. The wings of females of some *Accipiter* hawk species are nearly a quarter longer than those of males (Brown and Amadon 1968). Thus, artificial female/male averages often represent a phenotype that does not occur in nature. A more biologically realistic approach is to treat sexually dimorphic species as two "morphospecies" in null models (e.g., Dayan, Simberloff et al. 1989).

Geographic variation in size, independent of sexual dimorphism, has also been neglected in null model studies. Populations of vertebrates often differ significantly among islands, reflecting genetic adaptations to local environments. Randomization algorithms should sample distinctive phenotypes that occur on islands within the source pool area (e.g., Losos 1990). In most cases, this task has been accomplished by choosing among mean values of morphological traits for island populations (see Strong et al. 1979; Case and Sidell 1983).

Accounting for geographic variation in size of mainland source pool species is more difficult. Among mainland bird species, whose populations are more or less continuously distributed, morphological variation is usually clinal (James 1982). "Average" phenotypes of morphological characters may differ significantly between source pool areas of distantly separated land-bridge islands. In some cases, significant patterns of geographic variation may occur *within* a circumscribed source pool. If morphological clines are steep, the "average" bill size for the source pool would most likely characterize only a fraction of the source pool populations. In other words, use of source pool averages for highly variable species is equivalent to reducing the size of the source pool.

If care is not taken, size averaging procedures can yield rather uninterpretable results. For instance, in calculating the sizes of geographically variable species of sympatric bird-eating hawks, Schoener (1984) first identified the two subspecies with the largest geographic ranges in Brown and Amadon (1968). He then averaged the mean wing length of males and females to produce a subspecies average for each of the two subspecies. Lastly, the subspecies averages were averaged to produce a single value for each species. Use of this measure of body size was further complicated by Brown and Amadon's (1968) original size data, which often consisted only of the range of wing measurements for each sex of each subspecies (no sample size or mean). Additionally, the number of subspecies (and the morphological variation among subspecies) of hawks varies greatly among species. The degree of sexual dimorphism also varies geographically, as does size within subspecies. Many of the sympatric bird-eating hawks occur in the tropics, where the size of geographic ranges is smallest and morphological variation from subspecies to subspecies is often pronounced. Yet, for several species with large latitudinal ranges, Schoener's (1984) species-specific average was calculated from the size of temperate zone subspecies.

As we explained earlier, the resulting "average" may bear little resemblance to the population in a particular raptor community. Schoener (1984) has acknowledged some of these criticisms, but they make it difficult to interpret the significance of his results (Wiens 1989). Similar criticisms have been directed toward other studies of character displacement (see Grant and Abbott 1980; Hendrickson 1981).

To combat "averaging" bias, we recommend that null ratios be computed by sampling from normal distributions of the morphological characters bracketed by the observed extremes for source pool populations. Sexual differences can be accommodated by sampling each sex separately. Utilizing a normal distribution of body sizes sampled from a known geographic locale preserves the geographic variation in body size that is inherent in mainland faunas.

DATA QUALITY

Large-scale biogeography is largely an armchair pursuit; the vast majority of studies are derived from data originally published for other purposes. An alarming number of studies are based on compilations and catalogs, without direct reference to original sources or specimens. Notwithstanding the emphasis placed on Monte Carlo and statistical methods in most recent discussions, data quality remains the most important component of null models. It is the

data, after all, that are of primary interest, not the algorithm. In other words, a null model is only as good as the data it purports to evaluate. Unfortunately, there seem to be few quality control standards in the discipline.

We foresee an ominous trend in large-scale biogeography due to newly available electronic databases (e.g., US and Canadian Wildlife Service Breeding Bird Survey), compilations (e.g., Dunning 1993), checklists (e.g., Howard and Moore 1984; Sibley and Monroe 1990), and atlases (e.g., Root 1988c). Our concern lies not with the proffered convenience of new reference works, but with the fact that biologists who utilize these as their primary sources are at least twice removed from the raw data—some bird mass data in Dunning's (1993) handbook are thrice removed from the primary source! The methods, assumptions, and caveats expressed by the original authors, as well as an accounting of measurement and transcriptional error, are rarely presented in secondary data sources. Many users who cite compilations as their primary data never bother looking up the original sources.

We expect the naive use of biogeographic data by spreadsheet wizards to accelerate with the increasing availability of electronic data sets. We suggest, however, that data compilations should be used in the same fashion as a telephone directory, as a guide to the literature rather than a substitute for it. If ecologists lack personal experience with the species, habitats, and islands they wish to study, they should seek out expert collaborators for null model analyses! Poorly prepared and documented null models invite reanalysis and rebuttal. At least part of the contentious legacy of null model analysis in ecology is due to a cycle of weak publication and vitriolic rebuttal, *post hoc ergo propter hoc.*

This has been especially true in avian ecology. We believe that currently available data are probably insufficient to adequately test a number of famous biogeographic hypotheses, including the "taxon cycle" of West Indian birds (Ricklefs and Cox 1978), the existence of Pleistocene "refuges" for South American birds (Haffer 1974), and competitively driven extinctions of the Hawaiian avifauna (Moulton and Pimm 1983). We recommend that investigators routinely discuss and defend the sufficiency of their data for hypothesis testing.

HUMAN-CAUSED EXTINCTIONS ON ISLANDS

The classic works of island biogeography (e.g., MacArthur and Wilson 1967) were predicated on observations of "natural" communities—that is, islands with intact biotas. It has become abundantly clear in the past two decades that

extant island biotas are not what they seem. Human-caused extinctions, commencing with the arrival of Polynesians and continuing through the present, have been reported on every large oceanic island in the Pacific intensively studied by paleontologists and archaeologists (e.g., Olson and James 1982; Steadman 1989). The discovery of numerous extinct subfossil vertebrates in cultural contexts in the West Indies, Mediterranean islands, and Madagascar suggests that this generalization can be extended to all islands reached by Stone Age humans (Martin and Klein 1984). Extinctions were caused by direct predation by humans, habitat destruction, and the introduction of other predators, such as rats, dogs, and pigs (Case et al. 1992).

The avifaunas of some isolated archipelagoes have suffered catastrophic declines of more than 50% in species number (e.g., the Hawaiian Islands and New Zealand). Prehistoric extinctions have caused puzzling distributional gaps in certain groups of birds (e.g., pigeons, parrots, flightless rails) that in light of paleontological research are seen as artificial (Steadman 1989). Most volant species of birds currently restricted to a single Pacific island had more extensive prehistoric distributions. Other species of animals and plants are likely to have been influenced by this wave of destruction as well.

Do these discoveries invalidate the empirical underpinnings of classical island biogeography? The answer, of course, depends upon the taxon and the island. However, enough paleontological evidence for birds, mammals, and reptiles has been gathered to cast doubt on some venerable biogeographic icons, such as species-area and immigration-extinction relationships for those taxonomic groups. Some contemporary studies (e.g., Juvik and Austring 1979) have been rendered obsolete by recent paleontological studies (James and Olson 1991; Olson and James 1991). The emerging paleontological evidence must be eventually reckoned with in island biogeographic and null model studies.

CETERIS PARIBUS

The *ceteris paribus* ("all other things being equal") clause of null models deserves strong scrutiny. Other things in island biogeography are never equal. The biotic characteristics of islands are seldom equal (habitat, species composition, etc.), human influence is rarely equal (e.g., extinctions, alteration of habitats), and physical factors are never equal (size, shape, elevation, rainfall, etc.). These differences in islands need to be incorporated into statistical tests for distribution patterns (Schoener and Adler 1991). For example, mutually exclusive distributions of island bird species ("checkerboards") are often inter-

preted as the result of interspecific competition (Diamond 1975). Of the several *ceteris paribus* assumptions in such an analysis, the two most important are that adequate amounts of the preferred habitats for each species occur on every island, and that historical constraints on dispersal or extinction have not caused the patterns. Yet, the implications of such assumptions are rarely discussed in detail.

QUESTIONS IN NULL MODEL STUDIES

We suggest that ecologists ask themselves the following questions before submitting the results of a null model study for publication:

1. *Were the species data (measurements, geographic distributions, habitat, etc.) of high quality and derived from personal field work, specimens, or original literature sources?*
2. *Were source pools constructed with a standardized methodology, taking into account the spatial distribution of habitats and resources?*
3. *Was the null model used appropriate for the question at hand, and was it thoroughly described in the methods so that others could use it?*
4. *Was the computer implementation of the null model checked for programming errors and was it tested with idealized data sets?*
5. *Were the* ceteris paribus *assumptions defended and discussed?*
6. *Will source pool and island species data be published or deposited in a databank for public access?*

Although some of these questions are unique to null model studies, most are appropriate for any biogeographic study that is conducted at large spatial scales and relies on nonexperimental data. If the answer to these questions is not an unqualified "yes," the author should reconsider whether the study is worthy of publication. We encourage authors, reviewers, and editors to maintain quality control by considering these requirements.

THE FUTURE

The lack of commercially available computer software has hindered the growth of null modeling in ecology. The null model approach to ecological problems

has thus been the domain of computer-literate ecologists. Few ecologists are skilled enough to write complex algorithms, and even fewer computer programmers are knowledgeable in ecology. One needs to be accomplished in both disciplines in order to construct a useful null model. For this reason alone, we encourage collaborative efforts between computer-literate ecologists and data-oriented systematists.

Most biologists who currently use null models in ecology also write and understand the behavior of their own computer programs. This situation will change in the next decade as null model software tailored for ecological problems is developed and distributed. We see both benefits and disadvantages in this advancement. Wide public access to null model software will do for null models what the introduction of statistical software did for the rest of ecology—it will stimulate the routine application of null model analyses to nonexperimental ecological data and allow more kinds of biologists to use null models than have done so in the past. But it will also spawn a surfeit of studies in which the algorithms are inappropriately and indiscriminately applied to data. Be that as it may, the worm has turned. We hope the suggestions in this Epilogue and the recommendations at the end of each chapter will at least serve to increase the quality of future null model studies.