AVIFAUNAL EQUILIBRIA AND SPECIES TURNOVER RATES ON THE CHANNEL ISLANDS OF CALIFORNIA

BY JARED M. DIAMOND

PHYSIOLOGY DEPARTMENT, MEDICAL CENTER, UNIVERSITY OF CALIFORNIA, LOS ANGELES

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Abstract.—Insular species diversities, and their dependence on island size and isolation, have been postulated to represent a dynamic equilibrium between species immigration rates and species extinction rates. This interpretation has been tested by determining the land and freshwater birds breeding on the nine Channel Islands off southern California in 1968 and comparing the results with a similar survey for the years up to 1917. Most of the islands were found to be in equilibrium as to number of species, but between 17 and 62 per cent of the 1917 breeding species had disappeared by 1968, and an approximately equal number of new immigrant species had become established. Percentage turnover rates vary inversely as insular species diversities, with no effect of distance apparent.

One of the basic facts of island biology is that if the number of species of animals or plants are compared in similar habitats on different islands, fewer species are found on small or remote islands than on large islands or islands near the mainland. To explain this fact, MacArthur and Wilson[1] have suggested that the number of species on an island represents an equilibrium determined by the balance between immigration rates and extinction rates. Isolated populations fluctuate in size and may become extinct due to such random factors as disease, predation, or a transient decrease in food supply. The smaller the population, the higher the probability of extinction within a given time span. On the other hand, islands continually receive immigrants due to the random dispersal of animals or plants from the mainland or other islands. The nearer an island is to the mainland, the higher the immigration rate. Thus, island faunas should be in dynamic equilibrium, and the turnover rates (extinction rates or immigration rates, which are equal in the steady state) would be expected to decrease with increasing distance from the mainland and increasing island size.

To test this important generalization and to measure actual turnover rates in nature, one requires a group of islands which differ from each other in size and in distance from the mainland and which have been adequately surveyed with respect to some group of animals or plants at some time in the past. Such an opportunity is provided by the land and freshwater birds of the Channel Islands off southern California. This archipelago consists of nine islands or island groups which vary in size from 1.0 to 96 square miles and lie at distances varying from 8 to 61 miles from the mainland (Table 1, columns *A* and *B*). The results of a series of bird surveys in the years prior to 1917 were summarized by Howell.[2] Between March and August of 1968, I visited each island one to three times to determine the breeding land and freshwater bird species for comparison after this interval of 51 years.

Before discussing the results, three problems relevant to the interpretation of the results must be considered: the completeness of the surveys, habitat differences among the islands, and habitat changes resulting from human activities.

Howell considered that the pre-1917 surveys were adequate for all the islands except Santa Rosa and perhaps San Miguel. Howell himself spent periods of at least several weeks on each island, and the islands were also visited and systematically surveyed by other observers. The surveys of Santa Rosa and possibly of San Miguel were considered incomplete because it was difficult to obtain visiting permission from the owners of these two islands. In the present survey the very generous cooperation of many individuals plus the availability of jeep transport on the larger islands made it possible to survey most parts and all major habitat types of all islands. On each island I have been able to compare and supplement my own surveys with those of other observers stationed on the island for longer periods; hence, few breeding species are likely to have been missed in 1968. Both in 1917 and in 1968, cases arose in which a species was present on a certain island during breeding season and was suspected of breeding but proof in the form of a nest was not obtained. In such cases an arbitrary decision has had to be made on the basis of the available information as to whether the species probably was or was not breeding.

Regarding habitat differences among the islands, the aforementioned predictions derived from MacArthur and Wilson's theory concerning the dependence of species diversity and turnover rates on island sizes and distances apply to the simple case of a group of ecologically similar islands. However, there are ecological differences among the Channel Islands. Coastal sage scrub is the sole important habitat type on San Miguel, Santa Barbara, Los Coronados, and San Nicolas, and also occupies much or most of the area of the other islands. In addition, trees (particularly *Quercus* sp., *Lyonothamnus floribundus*, *Prunus ilicifolia*, and *Heteromeles arbutifolia*) are present in ravines on San Clemente and Anacapa. The next stage of habitat complexity is represented by Santa Catalina, Santa Cruz, and Santa Rosa, the three largest islands, which have not only trees in ravines but also significant areas of arborescent chaparral 10–30 feet high. Finally, pine forest (*Pinus remorata* and *P. torreyana*) occurs on Santa Cruz (the largest island) and Santa Rosa (the second largest island). Associated with the three richer habitat types on the islands (ravine groves, chaparral, and pine forest) are some bird species absent in coastal sage scrub.

The third factor that must be borne in mind in interpreting the results is that, beginning in the 19th century, ecological changes associated with European man have affected all the islands. In particular, the introduction of browsing animals, and in some cases, the subsequent removal of these animals, have modified the vegetation to varying degrees. The most marked changes in the original vegetation had already taken place in the 19th century, so that the comparison between 1917 and 1968 is not one between an undisturbed state and a disturbed state but between two disturbed states. The island for which ecological changes between 1917 and 1968 were most significant is probably Santa Barbara, which suffered a heavy fire in 1959.

Table 1 summarizes the results of the 1917 and 1968 surveys and the numbers of extinctions and immigrations implied by differences in the species found by

TABLE 1. *Avifaunal turnover on the Channel Islands.*

	Area A	Distance B	1917 species C	1968 species D	Extinctions E	Additions F	Introductions G	Immigrations H	Turnover I
Los Coronados	1.0	8	11	11	4	4	0	4	36
San Nicolas	22	61	11	11	6	6	2	4	50
San Clemente	56	49	28	24	9	5	1	4	25
Santa Catalina	75	20	30	34	6	10	1	9	24
Santa Barbara	1.0	38	10	6	7	3	0	3	62
San Miguel	14	26	11	15	4	8	0	8	46
Santa Rosa	84	27	14	25	1	12	1	11	32
Santa Cruz	96	19	36	37	6	7	1	6	17
Anacapa	1.1	13	15	14	5	4	0	4	31

For each island, column A gives the area in square miles; B, the distance in miles from the nearest point on the mainland; C, the number of species of land and freshwater birds breeding in 1917; D, the number of breeding species in 1968; E, the number of species that were breeding in 1917 but not in 1968 and hence must have gone extinct in the interim; F, the number of species breeding in 1968 but not in 1917 ("additions"); G, the number of species present in 1968 that had been successfully introduced by man between 1917 and 1968 (all of these are game birds: California quail, Gambel's quail, pheasant, or chukar); H, the number of species present in 1968 but not in 1917 that had immigrated under their own power between 1917 and 1968, calculated as F minus G; and I, the turnover rate expressed in per cent of the species pool per 51 years, calculated as $100\ (E + H)/(C + D - G)$.

these two surveys. The following conclusions may be drawn from the surveys and from the information in Table 1:

(1) Both in 1917 and 1968 certain bird species which are abundant on the adjacent mainland were absent from insular habitats with the same vegetational physiognomy and the same or similar plant species. Examples of bird species missing from all islands despite suitable habitat on many islands include the wren-tit, brown towhee, California thrasher, plain titmouse, and Nuttall's woodpecker. Some other species were present on the mainland and on certain islands in 1917 and 1968 but were absent from other islands with comparable habitat. For example, the scrub jay is present in chaparral, pine forest, and ravine groves on Santa Cruz but is absent from similar habitats on Santa Catalina, Santa Rosa, and Anacapa. Some species absent from suitable insular habitats in 1917 were present in 1968 and must have immigrated during the intervening period. For instance, the acorn woodpecker, a characteristic bird of large oaks, was present on Santa Catalina and Santa Cruz in 1968 but not in 1917. It is so noisy and conspicuous that it could not have been overlooked in 1917 if it had been present, and the colonization is known to have occurred in the late 1920's. Finally, some species present in insular habitats in 1917 were absent in 1968 despite ample areas of habitat characteristic of that species. For instance, the bush-tit, one of the two commonest insectivorous gleaners of mainland chaparral, was found in the chaparral of Santa Catalina before 1917 but was absent in 1968, although much of Santa Catalina remains ideal bush-tit habitat and the species is still common in similar habitats on Santa Cruz. These examples are typical of the random element so characteristic of insular zoogeography: that, although different species show inherent variation in their dispersal abilities, population densities, and population stabilities permitting statistical predictions of species colonizing abilities and island species diversities, there remains a large random element in the colonization of islands and in the extinction of isolated small populations.

(2) On every island some breeding species present in 1917 had become extinct

by 1968, while other species present in 1968 had been absent in 1917 and must have immigrated. For instance, on Los Coronados the peregrine falcon, Allen's hummingbird, barn swallow, and raven became extinct, while the sparrow hawk, black phoebe, house wren, and chipping sparrow immigrated. Despite this turnover, as a result of which the *identity* of 17 to 62 per cent of the species on each island changed, the total *number* of species remained constant within 16 per cent or less on six of the islands (compare columns *C* and *D* of Table 1 for Los Coronados, San Nicolas, San Clemente, Santa Catalina, Santa Cruz, and Anacapa). The recorded number of species increased grossly on Santa Rosa (from 14 to 25) and less so on San Miguel (from 11 to 15), but these increases are undoubtedly an artifact of the 1917 censuses, which Howell considered incomplete for these two islands. The only island on which there appears to have been a genuine large change in the number of species is Santa Barbara (decrease from 10 to 6), which lost much of its vegetation and presumably many of its birds in the 1959 fire. Thus, the postulate that insular species diversity represents a dynamic equilibrium is valid for the birds of the Channel Islands.

A few of these extinctions and immigrations are due to ecological changes caused by man. The disappearances of the bald eagle, osprey, and peregrine falcon from all islands on which they were formerly present occurred over the same time span as their disappearance from the southern California mainland and are generally attributed to the introduction of insecticides into their food chains. The establishment of the coot, which breeds on bodies of fresh water, as a breeding species on Santa Catalina was made possible by the construction of a freshwater reservoir in the 1920's. However, detailed examination of what species arrived or became extinct on each island indicates that such species changes due to changing habitats or effects of man are greatly in the minority. The changes are not systematic ones by habitat, i.e., it is not that chaparral birds have in general gained at the expense of grass birds, but rather that each habitat has gained and lost species. Cases of one-to-one replacement, in which the arrival of an immigrant is balanced by the disappearance of a close relative, are rare. The bird turnover rate on Los Coronados, on which habitat changes between 1917 and 1968 were less marked than on some other islands, is not particularly low but falls in the middle of the rates for all the islands. Many of the extinctions involved populations that were sparse or local in 1917 and were therefore the most likely to disappear as a result of accidents or fluctuation in numbers. One can never be certain that turnover rates were not significantly increased by effects of man, but the detailed results do make this unlikely.

(3) Percentage turnovers have been calculated for each island in column *I* of Table 1, as 100 times the number of extinctions plus the number of immigrations divided by twice the average number of species present in 1917 and 1968. This figure gives the percentage of the species on an island that changed identity in 51 years. Calculated turnover rates for 51 years vary from 17 per cent for Santa Cruz and 24 per cent for Santa Catalina, the islands with the most stable avifaunas, to 50 per cent for San Nicholas and 62 per cent for Santa Barbara, the islands with the least stable avifaunas. The simplest expectation derived from the model of MacArthur and Wilson was that these percentage rates should

decrease with increasing island size and increasing distance from the mainland. Study of Table 1 shows that these predictions are not fulfilled. For instance, San Nicolas is the most distant island and is of medium size and should, therefore, have had a low turnover rate, but it actually has the second highest rate. Anacapa and Los Coronados are the two islands nearest the mainland and are two of the three smallest and should, therefore, have had the highest turnover rates, but they actually have intermediate rates. However, there is a nearly perfect inverse correlation, illustrated in Figure 1, between percentage turnover rate and number of species on each island: the greater the number of species, the more stable the avifauna. Thus, Santa Cruz, with the largest number of species, has the lowest percentage turnover rate, while San Nicolas and Santa Barbara, with the fewest species, have the highest turnover rates. Arranging the islands in order of increasing species number(average of column *C* and columns *D* minus *G*) yields the same sequence as that of decreasing percentage turnover rates, except that the positions of Santa Rosa and Anacapa and of San Miguel and Los Coronados are inverted (due presumably to the inadequate 1917 survey of Santa Rosa and San Miguel and hence to the overestimated immigration rates on these two islands). There is evidently no effect of distance on turnover rates, since close and distant islands fall on the same nearly monotonic correlation curve of Figure 1.

There are two reasons for this initially surprising pattern of the turnover rates. First, the absence of a distance effect implies that dispersal distances of the bird species that colonized the islands are large compared to the distances of the Channel Islands from the mainland (up to 61 miles)—i.e., a potential colonist leaving the mainland, if capable of dispersing over water at all, has almost as good a chance of reaching the farthest island (San Nicolas, 61 miles out) as the nearest island (Los Coronados, 8 miles out). This conclusion is supported by the available evidence. The Channel Island archipelago lies in an indentation in the Pacific coastline and constitutes a flyway, such that north-south migrants along the California coast cross the ocean over the entire breadth of the archipelago. During migration peaks an observer in a boat at sea encounters migrants over open water at any point within or beyond the archipelago. The island distances

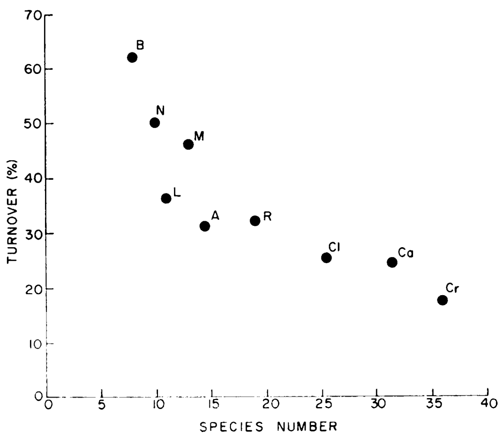

FIG. 1.—For each of the 9 Channel Islands, the ordinate gives the turnover rate of bird species, in per cent of the species pool per 51 years (column *I* of Table 1), while the abscissa is the number of species (average of column *C* and columns *D* minus *G*). Letters identify the islands: B = Santa Barbara, N = San Nicolas, M = San Miguel, L = Los Coronados, A = Anacapa, R = Santa Rosa, Cl = San Clemente, Ca = Santa Catalina, Cr = Santa Cruz. Note that the turnover rate varies inversely as the number of species.

are also small compared to the dispersal powers of California resident species which undertake radial postbreeding wanderings rather than north-south migrations. For example, since 1962 wandering individuals of the red-breasted nuthatch, mockingbird, and band-tailed pigeon have been recorded from the most distant island, San Nicolas, as well as from the nearer islands.

In the absence of a distance factor, why do turnover rates vary inversely with total species number but not simply with island size? If all islands had been ecologically similar, there should have been a close direct correlation between species number and island size, and a close inverse correlation between turnover rate and island size. In fact, however, the richer habitat types with more complex vegetational structure (pine forest, chaparral, ravine groves) are unequally distributed on the islands. On a single island, the numbers of bird species in different habitats correlate well with the vegetational complexity of the habitats.[3] A small island with rich vegetation is comparable to a large island with poor vegetation in terms of the populations and number of bird species it can support. Hence a good correlation between island size and turnover rate is to be expected only if size is weighted by some measure of vegetational complexity. Since island size is evidently related to turnover rate and to equilibrium species number by the same weighting factor, one observes a good empirical correlation between total species number and turnover rate (Fig. 1). For instance, San Nicolas is of medium size but is the poorest island in terms of vegetation and thus has the fewest bird species and highest turnover rate after Santa Barbara. If, at the other extreme, the islands had been similar in size and habitat and if the distance factor had been important rather than negligible, the relation between species number and turnover rate would have been direct rather than inverse.

Thus, there is no basic discrepancy between bird turnover patterns on the Channel Islands and predictions derived from equilibrium considerations. The turnover patterns are those expected for islands of varying ecology and for an animal group whose dispersal powers are large compared to island distances.

Finally, it should be remembered that the turnover rates of Figure 1 (17–62% per 51 years, or 0.3–1.2% per year) are minimal values because they were calculated on the implicit assumption that a species either remained on an island from 1917 to 1968, or became extinct and did not return, or immigrated and did not disappear again. In fact, available information for the islands from years between 1917 and 1968 shows that some species have immigrated and become extinct repeatedly on some islands. For instance, the burrowing owl occurred on Anacapa before 1917, was still present in 1939, was absent in 1963 and 1964, present again in 1967, and had disappeared again by 1968. Comparison of my 1968 surveys with surveys of particular islands carried out in the late 1950's and early 1960's (e.g., ref. 4) suggests that real turnover rates are in approximately the same sequence as the estimated rates of Figure 1, but that the real values are up to several times higher than the estimated ones, the effect being most marked for the least stable islands. For instance, comparison of the 1968 survey with a 1962 survey of San Nicolas,[4] the island with the second most unstable avifauna, yields a turnover rate of 4 per cent per year, instead of the value of 1 per cent per year derived from the 51-year comparison.

Ecological consequences of these insular invasions, extinctions, and variations in species diversity include striking expansions and compressions of the niche of a given species, depending upon the competing species pool it faces. Discussion of these niche shifts is reserved for a future report.

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