AVIFAUNA RICHNESS ON THE CALIFORNIA CHANNEL ISLANDS

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The familiar dynamic equilibrium theory of island biogeography (MacArthur and Wilson 1967) predicts that the equilibrial number of species on an island is a function of rates of immigration and extinction, which in turn are dependent on area and distance from a source of colonizers. A large island would tend to have greater habitat diversity supporting more species and would tend to have larger populations less prone to extinction than would a small island. Likewise, an island that is farther from a source of propagules is likely to have a reduced immigration rate of new species and hence a lower equilibrial species number than an island close to a source of colonizers.

The value of the dynamic equilibrium model is not currently in question, but there are still questions on the factors underlying the distribution of birds on the California Channel Islands (fig. 1), an archipelago often used in discussion of biogeographical processes. For example, Diamond (1969) reported that over a period of 51 years the numbers of bird species have remained relatively constant on the Channel Islands, while the species composition of avifaunas has changed, in some cases, markedly. The rate of turnover was found to be inversely correlated with the number of bird species present. Subsequently, however, a thorough reanalysis of Channel Islands bird data by Lynch and Johnson (1974) suggested that Diamond's turnover rates may have been inflated. In another case (Power 1972), I analyzed by multiple regression the numbers of bird species on 16 islands along the coast from Point Conception south to mid-Baja California. I found that variation in number of bird species was explained principally by number of plant species per island, which is an estimate of habitat diversity, and secondarily by average inter-island distance, a measure of isolation. Island area, a measure central to the dynamic equilibrium model, turned out to be a poor predictor of number of bird species, but was a good predictor of the number of plant species. Latitude, a measure roughly related to annual rainfall (Kimura 1974), also contributed to explanation of plant species. There has been some question, however, that with a more homogeneous subset of the islands, particularly the eight northernmost ones off Southern

California, island area might prove to be a more important independent variable. Weissman and Rentz (1976) have recently found that numbers of grasshopper species on the California Channel Islands are best explained by maximum island elevation and area, although it was not possible to clearly distinguish which might be the most important in terms of a causal relationship.

My own view has been that habitat diversity is the most important determinant of bird species richness on the California Islands. The distinction between area and habitat effects is important from a theoretical standpoint for they potentially account for different rate functions in the dynamic equilibrium model (Power, ms). I therefore believe that data on habitat diversity should be included in any biogeographic analysis of the kind we are dealing with here. Thus, even though the data on plants of the California Islands have been viewed with enough suspicion to be excluded from the grasshopper study of Weissman and Rentz (1976), in the present analysis I have obtained the best estimates available to me and included them in this new look at the species richness of land birds on the northern eight California Channel Islands.

DATA

Numbers of land bird species breeding on the Channel Islands are taken from three sources and will be treated separately.

Power's bird data (PB).—Numbers of species as used by Power (1972) and obtained from sources cited therein.

Diamond's bird data (DB).—Numbers of species as used by Diamond (1969).

Lynch and Johnson's bird data (LJB).—These are PB with species removed by the criteria of possibly not breeding as applied by Lynch and Johnson (1974).

Numbers of plant species (P).—Numbers of native plant species for San Miguel, Santa Rosa, Santa Cruz, and Anacapa islands are from R. Philbrick (pers. comm.) who based his counts on his own field work and collections in the Santa Barbara Botanic Garden herbarium. Most are more conservative than those by Johnson et al. (1968). Data for other islands are as follows: Santa Barbara (Philbrick 1972), Santa Catalina (Throne 1967, 1969), San Clemente (Raven 1963 and Thorne 1969), San Nicolas (Foreman 1967).

Area (A).—Island area (km^2) is from Philbrick (1967), with that for Anacapa being a sum of the areas of the three islets.
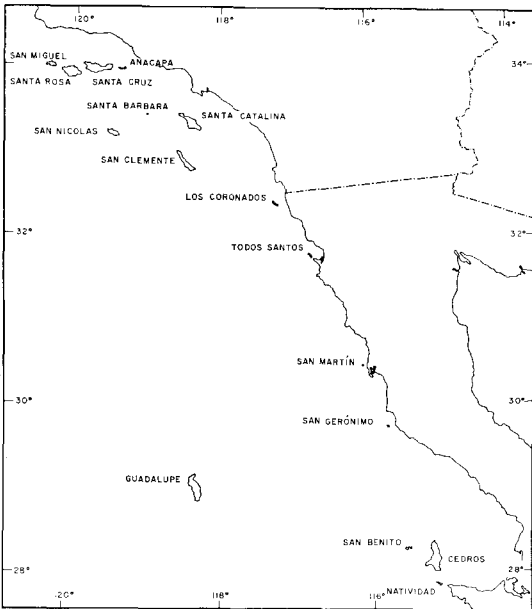
FIGURE 1. Map of the California Islands. The present study centers on the avifaunas of the northern eight Channel Islands.

Elevation (E).—Elevation (m) to the highest point; data are from Weissman and Rentz (1976).

Topographic diversity index (TD).—The number of arroyos per kilometer of coastline; data are from Weissman and Rentz (1976) and justification for the use of *TD* is cited therein.

Latitude and a number of isolation indices used in my 1972 analysis are not repeated here. Correlation coefficients between bird data and those indices are much smaller than those to be reported for variables listed above.

ANALYSIS

Variables in table 1 were subjected to correlation analysis (table 2). The best predictors of number of bird species are clearly elevation and number of plant species, regardless of the source of the bird data. Island area is also a very good predictor, but less so than elevation and plant diversity. The topographic diversity index falls short; if this were a sample from a large population, and the correlation coefficients for *TD* tested for

TABLE 1. Data on the Channel Islands (see text for explanation of variables).

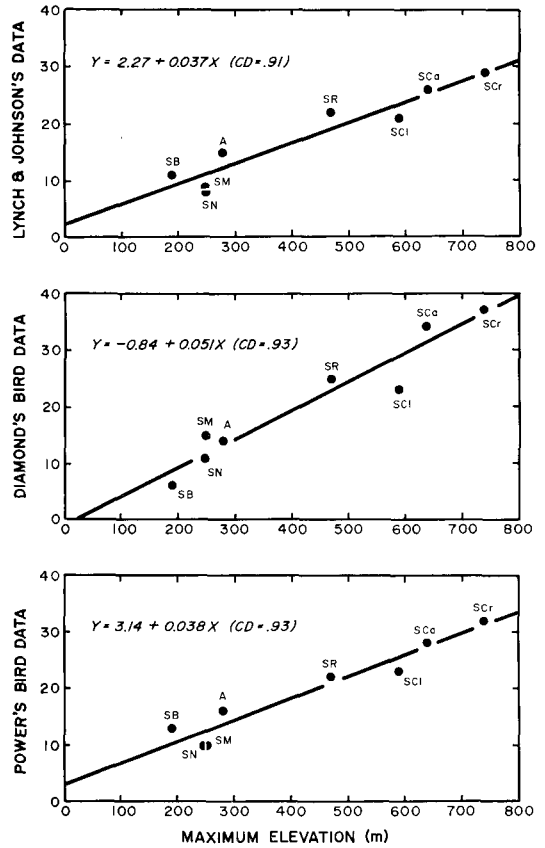| Island	PB	DB	LJB	P	A	E	TD
San Miguel	10	15	9	149	37	249	0.76
Santa Rosa	22	25	22	229	217	468	1.14
Santa Cruz	32	37	29	367	249	741	1.45
Anacapa	16	14	15	157	2.9	279	0.46
San Nicolas	10	11	8	94	58	249	0.85
Santa Barbara	13	6	11	68	2.6	191	0.58
Santa Catalina	28	34	26	396	194	638	0.83
San Clemente	23	24	21	239	145	590	1.22

FIGURE 2. Regressions of number of land bird species breeding on the Channel Islands (three estimates) on maximal island elevation. CD = coefficient of determination or r^2.

significance, only $r_{TD \cdot DB}$ would be significant at $P < 0.05$. Regressions of bird data on elevation and on plant diversity show the close fit between the variables (figs. 2 and 3). There is little difference among the three estimates of bird species numbers.

With a sample size of only eight, multiple regression analysis is not reliable. We are therefore limited to series of simple regressions with no statistically reliable way to cor-

TABLE 2. Product-moment correlations among variables.[1]

	PB	DB	LJB	P	A	E	TD
PB	—						
DB	.94	—					
LJB	.99	.94	—				
P	.93	.98	.93	—			
A	.88	.92	.89	.86	—		
E	.96	.97	.95	.94	.91	—	
TD	.69	.73	.68	.61	.86	.81	—

[1] Data for these correlation coefficients are from a statistical population, not a sample, so a test of significance is not appropriate. However, for a sample with $n = 8$ a significant r at $P < 0.05$ is .707 and for $P < 0.01$ is .834.
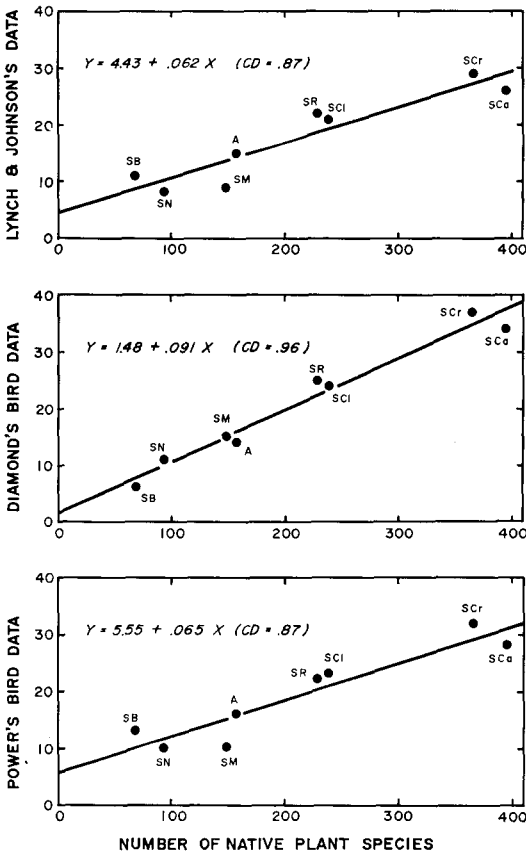
FIGURE 3. Regressions of number of land bird species breeding on the Channel Islands (three estimates) on number of native plant species. CD = coefficient of determination or r^2.

rect for correlations among independent variables.

DISCUSSION

The present analysis shows that variation in number of land bird species breeding on the eight Channel Islands off southern California is accounted for primarily by variation in maximum elevation of islands and number of native plant species. These measures account for critical aspects of habitat diversity and are logically related. Greater elevational variation would increase substrate and climatic variation, and these in turn would effect variation in plant species. Significant interrelationship of habitat characteristics and bird distribution on islands has been found by

TABLE 3. Selected data for Guadalupe and Cedros islands, Baja California.

Island	PB	P	A	E
Guadalupe	12	163	254	1402
Cedros	12	205	347	1204

many other workers (e.g., Crowell 1963, Diamond 1970a, 1970b, 1973, Grant 1969, Keast 1970, Lack 1969a, 1969b, 1970, Power 1972, 1975, Yeaton 1974). Possibly, elevation may also be tied in with area in indicating surface area; a larger surface area would tend to harbor larger populations less prone to extinction than would islands with a smaller surface area, resulting in increased species diversity.

The role of area (A) seems less certain. Clearly this variable is highly correlated with bird species diversity (B), but it is also highly correlated with island elevation (E) and plants (P). It is therefore uncertain whether the high correlation (r) between B and A indicates a casual pathway or is a secondary effect of r between P and A and between E and A.

It is useful to compare the present results with those of other studies that have found elevation to be important. Harris (1973) applied a multiple regression analysis to recent data on numbers of land birds of the Galápagos Islands and found that the number of plant species is the primary independent variable, with maximum elevation as the secondary and only other factor of importance, even though area and inter-island distance measures were also included in the statistical treatment. In a related study, (Power 1975), I showed that similarity among Galápagos avifaunas is accounted for primarily by variation in the similarity in composition of island floras, and, to a much smaller degree, by isolation among islands. Size, position, and wind patterns are also suspected of having an influence in the Galápagos.

It is well known that ecological segregation of species often follows elevation on islands as well as continents (e.g., Diamond 1973, Terborgh 1971). Increased ecological segregation among species owing to extreme elevation would lead to an increase in total number of species on an island. Lack (1973) considered elevation to be an important determinant of the numbers of hummingbird species on certain West Indian islands. Although a species-area relationship exists, Lack concluded (p. 335), "the number of species of hummingbirds on each island has been determined primarily by ecological factors, in particular the availability of habitats, and not by difficulties of dispersal." He went on to state (p. 336), "The number of species of hummingbirds on each West Indian island is correlated with altitude, mainly because montane humid forest brings in an additional species." Thus, even though elevation is the
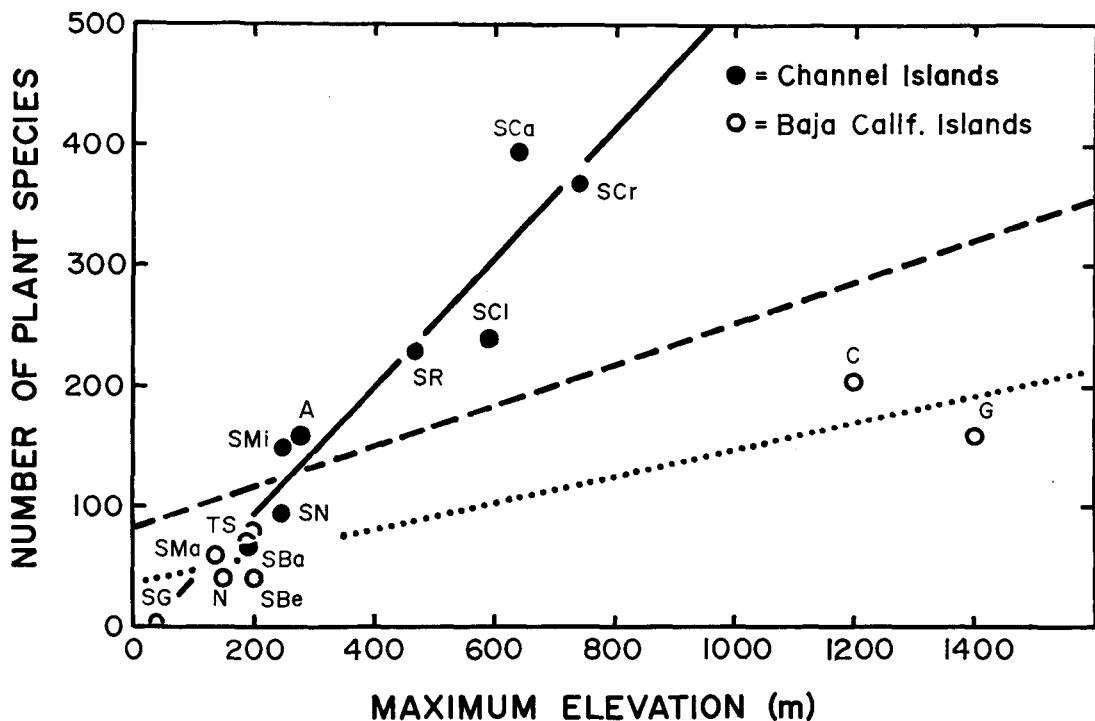
FIGURE 4. Regression of number of native plant species on maximum elevation for the Channel Islands only (solid line), the entire collection of California Islands (dashed line), and the Baja California Islands only (dotted line). Note that Guadalupe (G) and Cedros (C) fall well below the estimated plant-elevation relationship obtained for the northern islands.

measured trait, habitat factors consistently appear to be the causal ones.

There remains to be discussed the comparison of my earlier study of all 16 of the California Islands with the present analysis of the eight northern Channel Islands, the principal difference being that elevation figures into this study while it did not in the earlier one. The Channel Islands are a much more homogeneous subset of the entire group, being contained within an area about 2° of longitude and latitude square. Although those islands at the southern extreme of the northern set tend to be somewhat warmer and more arid (Kimura 1974), climatic differences are not extreme. This is not the case when the Baja California islands are included, for with these there is considerable extension southward. Distances between the extreme islands are almost 3.5 times greater with the set of 16 islands than with the set of eight. Furthermore, six of the Baja islands are small, near-shore extensions of the coastal mainland, while two near the southern end of the chain, Guadalupe and Cedros, are especially large and high. Also, Guadalupe is an oceanic island, having no submerged continuation with a mainland mountain change.

With the Channel Islands, elevation closely tracks the critical habitat factors, while with the California Islands *in toto* it does not. The difference between variation in plant species and elevation becomes more obvious when we consider the relationship of one to the other (fig. 4). The correlation between these two variables is high ($r = 0.94$) when just the northern islands are considered. However with the entire set of all islands the correlation is much lower ($r = 0.58$). A deterioration of the positive relationship is due solely to the inclusion of the two largest Baja islands, Guadalupe and Cedros. Compare the data of table 3 with those for large northern islands in table 1. Guadalupe and Cedros, while large and reaching a high elevation, have few species of plants, owing in part perhaps to isolation, but principally to reduced rainfall in the more southerly latitudes. Thus, although these two islands are topographically diverse, they have a lower habitat diversity than many medium-sized islands to the north. This supports the view that numbers of birds are primarily related to habitat diversity rather than elevation *per se*.

SUMMARY

Variation is analyzed in the numbers of land bird species breeding on eight Channel Is-

lands off the coast of southern California. Variation in maximum island elevation and numbers of native plant species are principal predictors of avian diversity. Island area is also highly correlated with number of bird species. A comparison is made with an earlier analysis of avian diversity on the California Islands, which include the Channel Islands plus eight more off the coast of Baja California. In this geographically and climatically more heterogeneous collection, numbers of plant species alone is most significant in explaining variation in number of bird species. Elevation and plant diversity are less highly correlated here owing to more arid conditions. Habitat diversity rather than elevation or area *per se* appears to be the primary factor accounting for avian diversity on the California Islands.

ACKNOWLEDGMENTS

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