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Author(s): A. Binion Amerson, Jr.

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## SPECIES RICHNESS ON THE NONDISTURBED NORTHWESTERN HAWAIIAN ISLANDS<sup>1</sup>

A. BINION AMERSON, JR.<sup>2</sup>

*Museum of Natural History, The University of Kansas, Lawrence, Kansas 66045 USA*

**Abstract.** An examination of selected ecological variables on the 18 low, sandy, non-disturbed islands of the northwestern Hawaiian Islands, and the vascular plants and birds, primarily seabirds, occurring there shows that species richness on low, sandy, oceanic islands is influenced by ecological diversity and is affected by variables similar to those on high, rocky islands. Species richness of vascular plants on these islands can be predicted by means of stepwise regression on the basis of area of vegetation, and to a lesser extent, elevation. In turn, variation in numbers of breeding species of seabirds, total species of seabirds, and total species of birds on these same islands can be predicted on the basis of number of species of vascular plants, and to a lesser extent, area of the island. Ecological diversity, although poor in quality, is of prime importance in regulating use of low, sandy, oceanic islands by any seabird. Although terrestrial birds use islands for obtaining food and for nesting whereas seabirds use islands only as a nesting and roosting place, species of terrestrial birds and seabirds on islands are associated with similar ecological variables.

**Key words:** *Atolls; biogeography; birds; diversity; Hawaii; Islands; Pacific; plants; seabirds.*

### INTRODUCTION

The detection and measurement of factors associated with numbers of island species has been a major activity of evolutionary biologists in recent years. The relation between area and biotic diversity was discussed in detail first by Arrhenius (1921) and most recently by MacArthur and Wilson (1963), MacArthur (1965), Vuilleumier (1970), and Terborgh (1973). Other workers, notably MacArthur and Wilson (1967) and MacArthur (1972), have shown that significant precision can be added by including other ecological, environmental, climatic, and isolational variables in their statistical analyses. These authors have used linear regression of both original variables and log transformations thereof, as well as multiple regression adaptations of these two, for studying numbers of plant and animal species.

All previous studies of this nature have concerned high, rocky islands, terrestrial plants, and terrestrial birds. This paper considers two basic questions not previously examined: (1) whether the same ecological variables interact in the same pattern to regulate species richness on low, sandy islands; and (2) because terrestrial birds use islands for obtaining food and for nesting while seabirds use islands only as a nesting place, whether species of terrestrial birds and seabirds on islands associate with similar ecological variables.

The present study examines ecological variables

on the low, sandy islands of the northwestern Hawaiian Islands and the species of vascular plants and birds, primarily seabirds, occurring there. These islands are well known botanically and zoologically from the extensive field work conducted in the central Pacific 1963-69 by the Pacific Ocean Biological Survey Program (POBSP) of the Smithsonian Institution, Washington, District of Columbia.

### MATERIALS AND METHODS

The Hawaiian Islands stretch for some 2,600 km in the central Pacific Ocean from Hawaii Island to Kure Atoll (Fig. 1). The archipelago is divided into the main Hawaiian Islands and the northwestern Hawaiian Islands, the latter—excepting Midway and Kure Atolls—being the Hawaiian Islands National Wildlife Refuge. I visited all islands in the Refuge on various dates from 1963 to 1969 while employed by the POBSP.

Of the 32 individual, named islands and islets in the northwestern Hawaiian Islands, 26 are low and sandy; 6 are high and rocky. Eight of these low, sandy islands have had a history of human disturbance causing wholesale depletion of seabird faunas and disruption of ecological relationships (Amerson 1973, King 1973). Human disturbance is herein defined as caused by inhabitation by man, by guano mining, and by introduction of foreign mammal and bird species (some of them predators) and plant species. Thus, because of human disturbance, only 18 low, sandy islands from two atolls, French Frigate Shoals and Pearl and Hermes Reef (Fig. 1, Table 1), are considered to be natural or non-disturbed. These islands are the concern of this study.

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<sup>2</sup> Present address: Environment Consultants, Inc., 14325 Proton Road, Dallas, Texas 75240 USA.

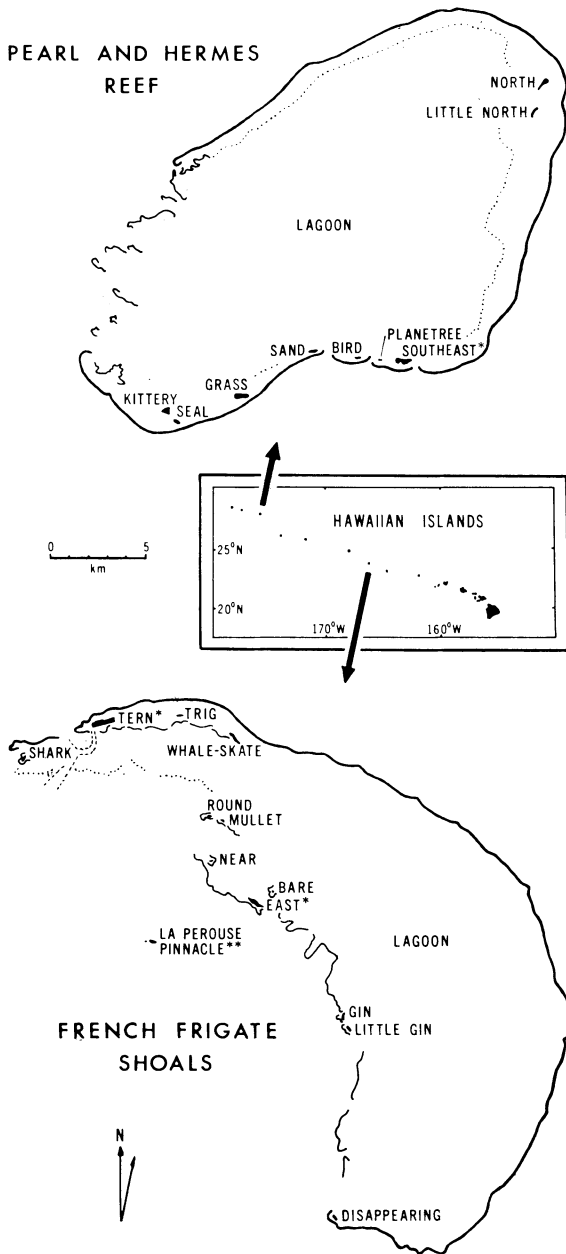


FIG. 1. The only low, sandy, nondisturbed islands in the Hawaiian Islands are at French Frigate Shoals and Pearl and Hermes Reef. \* Disturbed island. \*\* High, rocky island.

The ecological data, as well as the ornithological and botanical species data, presented here and summarized in Table 1, were assembled from natural history studies by Amerson (1971) and Amerson et al. (*in press*).

#### Ecological variables

The 18 islands considered are unique in that they are simple, noncomplex islands. They are low

( $\bar{x}$  = 2.4 m; SD = 1.6) and small ( $\bar{x}$  = 2.3 ha; SD = 2.3) and support few species of vascular plants ( $\bar{x}$  = 3.6 species; SD = 4.5). Thus, ecological diversity is poor when compared with the complex nature of most high, rocky islands.

Ten ecological measures (Table 1) were selected as independent variables. These were easily measured by use of aerial photographs, maps, and direct observations.

#### Avifauna and vascular flora

This paper deals only with the number of species—commonly referred to as species richness—recorded on each island. In all, 29 species of birds (excluding natural dispersal of known human introductions from nearby disturbed islands) are known from the 18 islands (Appendix I). Of the 29, 16 are resident breeding species of seabirds and 1 is a potentially breeding species of seabird; these are 2 albatrosses, 2 shearwaters, 2 petrels, 1 storm petrel, 1 tropicbird, 3 boobies, 1 frigatebird, and 5 terns. The more numerous breeding species are the Sooty Tern (*Sterna fuscata*), Black-footed Albatross (*Diomedea nigripes*), and Laysan Albatross (*D. immutabilis*), all of which are colonial and whose populations frequently number in the thousands. Of the remaining 12 species, 5 are regular migrant shorebirds whose breeding grounds are in the northern higher latitudes (1 plover, 1 curlew, 1 tattler, 1 turnstone, and 1 sanderling); 7 are vagrant or accidental sea and freshwater species (1 shearwater, 1 duck, 4 gulls, and 1 puffin).

Fifteen of the 18 species of known vascular plants are native to the 18 islands (Appendix II). The more common species are *Lepturus repens*, a grass, and *Tribulus cistoides*, a vine-like herb. Three non-native species—two grasses and one mustard—are known in small numbers on four islands; all three species are known from nearby disturbed islands.

The population characteristics selected as dependent variables were as follows:

SEAB: Number of species of seabirds breeding historically on the island: a measure of the actual breeding species of seabirds.

SEAT: Total number of species of seabirds known historically from the island: a measure of the actual plus potential breeding species of seabirds.

BIRDS: Total number of species of birds recorded historically from the island: a measure of total species of birds (seabirds, freshwater birds, and shorebirds).

PLS: Number of species of vascular plants recorded historically on the island: a measure of actual species of plants (when used as a de-

TABLE 1. Ecological variables and observed and predicted numbers of species of plants and birds<sup>a</sup> for 18 low, sandy, nondisturbed islands of the northwestern Hawaiian Islands

Island	LAT	LONG	DNI	DNVI	ANI	ANVI	AR	ARV	EL	PLS		SEAB		SEAT		BIRDS		
										Y <sub>1</sub>	Ŷ <sub>1</sub>	Y <sub>2</sub>	Ŷ <sub>2</sub>	Y <sub>3</sub>	Ŷ <sub>3</sub>	Y <sub>4</sub>	Ŷ <sub>4</sub>	
French Frigate Shoals																		
Bare	23.47	166.12	0.84	0.84	4.57	4.57	0.04	0.00	1.22	0	1	0	0	1	3	1	4	4
Gin	23.44	166.10	0.80	0.80	2.06	2.06	1.30	0.00	2.44	1	2	3	2	5	5	7	7	7
Disappearing	23.38	166.10	9.46	9.46	2.06	2.06	2.51	0.00	3.05	0	3	1	2	7	5	10	7	7
Little Gin	23.44	166.10	0.80	0.80	1.30	1.30	2.06	0.00	1.83	3	1	4	4	7	7	9	10	10
Mullet	23.49	166.14	0.56	0.56	0.20	0.20	0.20	0.00	1.22	0	1	0	0	2	3	2	4	4
Near	23.48	166.14	2.12	2.22	0.20	0.20	0.04	0.00	1.22	0	1	0	0	1	3	1	4	4
Round	23.49	166.14	0.56	3.80	0.20	6.80	0.20	0.00	1.22	4	1	4	3	7	6	10	8	8
Shark	23.51	166.20	3.89	3.89	22.99	22.99	0.32	0.00	2.44	1	2	0	1	5	4	5	5	5
Trig	23.52	166.15	2.32	2.32	6.80	6.80	4.01	1.86	6.10	9	12	10	10	15	13	23	19	19
Whale-Skate	23.51	166.13	2.32	2.32	4.01	4.01	6.80	2.63	3.05	8	10	13	11	16	15	23	23	23
Pearl and Hermes Reef																		
Bird	27.47	175.50	0.93	1.85	0.45	13.76	1.38	0.00	0.61	0	0	3	1	5	4	7	6	6
Grass	27.46	175.54	3.23	3.23	4.29	4.29	4.45	1.05	4.57	11	8	11	11	15	15	22	22	22
Kittery	27.46	175.56	0.47	0.47	4.29	4.29	4.82	0.00	1.52	0	1	3	4	7	8	12	11	11
Little North	27.54	175.44	0.77	0.77	6.43	6.43	0.57	0.20	3.05	4	4	3	3	6	6	12	9	9
North	27.56	175.44	0.77	0.77	0.57	0.57	6.43	2.87	3.05	12	11	11	13	16	18	23	26	26
Planetree	27.47	175.49	0.61	0.61	13.76	13.76	0.45	0.00	0.61	0	0	0	0	2	3	3	4	4
Sand	27.47	175.52	2.08	3.94	1.38	4.45	0.93	0.00	0.61	0	0	0	1	3	4	4	5	5
Seal	27.45	175.56	0.47	3.23	4.45	4.45	4.29	1.01	4.57	11	8	12	11	15	15	21	22	22
Mean	25.256	170.298	1.833	2.327	4.445	5.722	2.267	0.534	2.354	3.6	3.7	4.3	4.3	7.5	7.6	10.8	10.9	10.9
SD	2.052	4.793	2.164	2.186	5.720	5.819	2.280	0.959	1.554	4.5	4.1	4.8	4.6	5.4	5.1	8.1	8.1	7.7

<sup>a</sup> AR = area in ha; ARV = area of vegetation in ha; EL = elevation in m; LAT = latitude; LONG = longitude; DNI = distance to nearest island in km; DNVI = distance to nearest vegetated island in km; ANI = area of nearest island in ha; ANVI = area of nearest vegetated island in ha; PLS = species of plants; SEAB = breeding species of seabirds; SEAT = total species of seabirds; BIRDS = total species of birds; Y = observed; Ŷ = predicted.

TABLE 2. Correlation coefficients ( $r$ ) between ecological variables and number of species of plants and birds for 18 low, sandy, nondisturbed islands of the northwestern Hawaiian Islands. Table 1 describes the variables

	LONG	DNI	DNVI	ANI	ANVI	AR	ARV	EL	PLS	SEAB	SEAT	BIRDS
LAT	1.00**	-0.29	-0.21	0.01	0.13	0.26	0.11	-0.02	0.25	0.21	0.20	0.25
LONG		-0.28	-0.20	0.00	0.13	0.26	0.10	-0.02	0.24	0.20	0.19	0.25
DNI			0.89**	0.14	0.05	0.07	-0.03	0.26	-0.09	-0.09	0.08	0.05
DNVI				0.03	0.07	0.01	-0.08	0.21	-0.02	-0.03	0.12	0.08
ANI					0.82**	-0.16	-0.08	0.12	-0.08	-0.16	-0.07	-0.09
ANVI						-0.28	-0.21	-0.11	-0.20	-0.22	-0.16	-0.18
AR							0.84**	0.59*	0.74**	0.86**	0.89**	0.89**
ARV								0.61**	0.84**	0.86**	0.86**	0.84**
EL									0.78**	0.75**	0.81**	0.81**
PLS										0.94**	0.93**	0.92**
SEAB											0.97**	0.96**
SEAT												0.99**

\* Significant at the 0.05 level.

\*\* Significant at the 0.01 level.

pendent variable, deleted as an independent variable).

#### Analysis of data

To detect simple relationships among these variables, I first computed product-moment correlation coefficients ( $r$ ). To ascertain which of the independent variables contributed most to predicting species richness, and correcting for correlations among the various variables, I carried out stepwise regressions using BMDO2R computer program (Dixon 1970). The independent variable entered into the regression equation at each step was that which made the greatest reduction in the error sum of squares. I used the coefficient of multiple determination ( $R^2$ ) to estimate how much variance in the predicted values of the dependent variables was due to regression (Sokal and Rohlf 1969).

In my computations I used all 18 nondisturbed islands, and separately used the 8 nondisturbed islands at Pearl and Hermes Reef and the 10 at French Frigate Shoals.

In order to test the predictive value of the final multiple regression equation using all 18 islands, I selected a random sample of 12 islands from the 18. Data from this random sample were used to generate three new multiple regression equations, from which I then predicted values of the dependent variables for the remaining 6 islands. If the six predicted values generated from each of the new equations were not significantly different from the observed values, using the paired comparisons  $t$ -test (Sokal and Rohlf 1969), each equation using all 18 islands could then be judged as satisfactory.

## RESULTS

### Correlation among variables

Correlation coefficients ( $r$ ) among the nine ecological variables and four species richness variables

are presented in Table 2. Area of vegetation (ARV) is significantly correlated with area (AR) and elevation (EL). In addition, AR, ARV, and EL are each significantly correlated with numbers of species of plants (PLS), breeding seabirds (SEAB), total seabirds (SEAT), and total birds (BIRDS). Furthermore, PLS is significantly correlated with SEAB, SEAT, and BIRDS. SEAB, SEAT, and BIRDS are also significantly correlated with each other.

Latitude (LAT) and longitude (LONG) of the islands, the two measures of environmental and climatic variation, are significantly correlated with each other, being two tight clusters of islands behaving essentially as two single points. Likewise, distance to nearest island (DNI) and distance to nearest vegetated island (DNVI), as well as area of nearest island (ANI) and area of nearest vegetated island (ANVI)—the four measures of isolation—are, respectively, significantly correlated because most islands are vegetated.

### Stepwise regression analysis

Stepwise regression analysis using all 18 nondisturbed islands produced similar coefficients of multiple determination values and similar predictive results and significance for SEAB, SEAT, BIRDS, and PLS. Likewise, regression analysis using the 18 islands separated into their two respective atolls, and using the random sample of 12 islands, produced similar results, thus providing a positive check for the predictive value of each of the multiple regression equations. In addition, in each equation two variables accounted for 82%–95% of the variation, with all remaining variables combined contributing little (3%–10.5%) to the analysis (Amerson 1973). Because of these similarities, only results using all 18 nondisturbed islands and the two most important ecological variables are presented herein.

*Breeding species of seabirds.*—SEAB was posi-

tively correlated with PLS and AR, both statistically very highly significant (Table 3). The coefficient of multiple determination equaled 0.945, meaning 94.5% of the variation can be accounted for by the two independent variables chosen for the final linear regression equation:

$$(1) \quad \hat{Y}_{SEAB} = 0.09855 + 0.74472(AR) + 0.71627(PLS).$$

Substituting the observed independent variables in equation (1), I predicted SEAB for each of the 18 islands (Table 1). No significant differences were found.

The other eight variables contributed only an additional 3.1% to the variation (Amerson 1973).

*Total species of seabirds.*—SEAT was also highly correlated with PLS and AR (Table 3). The coefficient of multiple determination ( $R^2$ ) was 0.954. Thus 95.4% of the variation was accounted for on the basis of two independent variables entered in the final regression equation:

$$(2) \quad \hat{Y}_{SEAT} = 2.54276 + 1.04127(AR) + 0.73041(PLS).$$

Using equation (2), I predicted SEAT for each of the islands (Table 1); no significant differences were found.

Of lesser importance were DNVI, ANI, ANVI, EL, and LAT. These five variables combined, however, contributed only an additional 3.7% to the explained variation (Amerson 1973).

*Total species of birds.*—BIRDS highly correlated with PLS and AR (Table 3).  $R^2$  was 0.938. This shows that 93.8% of the variation was accounted for on the basis of two independent variables entered in the final linear regression equation:

$$(3) \quad \hat{Y}_{BIRDS} = 3.43876 + 1.60914(AR) + 1.05390(PLS).$$

Using equation (3), I predicted BIRDS for each of the islands (Table 1); no significant differences were found.

EL and ANI were of lesser importance, and added only an additional 3.5% to the variation (Amerson 1973).

*Total species of vascular plants.*—PLS was highly correlated with ARV, very highly significant, and to a lesser extent to EL.  $R^2$  was 0.815 (0.698 for area of vegetation and 0.117 for elevation). Thus, 81.5% of the variation was accounted for by two independent variables entered in the final linear regression:

$$(4) \quad \hat{Y}_{PLS} = -0.83878 + 2.68665(ARV) + 1.25655(EL).$$

Using equation (4), I predicted PLS for each of the

TABLE 3. Comparison of coefficients of multiple determinations ( $R^2$ ) for the two most important independent variables used in predicting SEAB, SEAT, and BIRDS using 18 low, sandy, nondisturbed islands of the northwestern Hawaiian Islands. All have significant  $F$ -ratio at  $P < 0.001$

Independent variable	$R^2$		
	SEAB	SEAT	BIRDS
Number of plant species	0.888	0.868	0.846
Area	0.057	0.086	0.092
Total $R^2$	0.945	0.954	0.938

islands (Table 1); no significant differences were found.

DNVI and DNI were of lesser value, adding only an additional 8.8% to the variation (Amerson 1973).

#### DISCUSSION

For land birds of the high, rocky islands of the West Indies, East Indies, various Pacific islands, Gulf of Guinea Islands, and páramo "islands" of the northern Andes (Hamilton et al. 1964, Hamilton and Armstrong 1965, Vuilleumier 1970) and for plants of the islands along the California coast (Johnson et al. 1968), area was the best single predictor of species richness when used in multiple regression analysis. Two exceptions were the land plants and the Darwin finches of the Galapagos Islands (Hamilton et al. 1963, Hamilton and Rubinnoff 1963, 1964, 1967), where plant species diversity was best predicted by elevation, and finch diversity by interisland distance.

Vuilleumier (1970) suggested that the two exceptions were atypical of archipelagos where the flora and fauna were well known, and concluded that area was generally the most important independent variable permitting prediction of the number of insular species.

Lack (1973) suggested that some land bird families may not follow the species-area curve. Terborgh (1973) found that species-area regressions for land bird families fall into four categories that reflect different family trends in dispersal ability, population density, and habitat requirements. Other variations have been noted by Diamond (1969, 1972).

In the present study, 2 of the 10 ecological variables were clearly able to predict, with a high degree of accuracy, SEAB, SEAT, BIRDS, and PLS (Table 1). Area alone was never the best single predictor for number of species, which differs markedly from Vuilleumier's conclusions. Thus there appears superficially to be a different relationship between ecological variables and numbers of plant and bird species on high, rocky islands and low, sandy islands.

The area of vegetation on an island was the best single predictor (69.8% of variance) for number of plant species. Elevation was second (11.7%), distance to nearest island third (4.1%), and distance to nearest vegetated island fourth (4.7%). Area of the island ranked eighth and last, at 0.1% (Amerson 1973). Because of the nature of stepwise regression (Draper and Smith 1966), most of the predictive power of area was used up by area of vegetation, since the two are highly correlated. Area of vegetation was not used as a predictive ecological variable in the studies cited previously. If area of vegetation, in addition to area, had been used in these studies, perhaps it, instead of area, would have been the best predictor. For predicting plant species on low, sandy islands, area of vegetation is definitely more important than area alone.

Although winter storms greatly affect the distribution and formation of islands in the northwestern Hawaiian Islands (Standen 1967, Amerson 1971, Amerson et al., *in press*), presence of vegetation and elevation are also very important in island formation. Vegetation, whether of one species or many, helps to stabilize low, sandy islands by providing root systems and necessary cover to hold the loose soil together. Elevation, the second best predictor for number of plant species, also involves stability. For low, sandy islands the higher an island, regardless of its size, the more physically stable it becomes. The more stable an island becomes, the more plant species it can support.

Data from Table 1 suggest that an island has to be a little over 1 m in elevation in order to support one plant species. The first plant species to colonize these minimal islands appear to be *Lepturus repens*, *Boerhavia repens*, *Portulaca lutea*, and *Tribulus cistoides*.

The number of vascular plant species was the single most important predictor for SEAB (88.8%), SEAT (86.8%), and BIRDS (84.6%). This agrees with Bowman (1961) and Lack (1969, 1971, 1973), who suggested that the numbers of land and freshwater bird species on islands are strongly correlated with number of plant species.

The present study also agrees with Power (1972), who found that numbers of land bird species breeding on islands off the coast of southern California and northwestern Baja California, Mexico, are largely accounted for by numbers of native plant species (67% of variance). Power further found that land bird species richness was influenced by degree of isolation, as measured by average interisland distance (14%), and by unknown factors (19%). In turn, numbers of plant species were explained primarily by island area (58%), by latitude (25%), and by unknown factors (17%). He concluded that island

area was a relatively poor predictor of numbers of bird species.

Of the 16 species of seabirds that breed on the low, sandy islands of the northwestern Hawaiian Islands, all but two—the Black-footed Albatross and Blue-faced Booby (*Sula dactylatra*)—usually nest in association with vegetation. These two seabird species are usually the only ones that will nest on islands devoid of vegetation. Because of the low number of plant species available on any island (Table 1), it is not surprising that the remaining species of birds utilize the plants fully. They nest in, on, and under the vegetation. Some bird species, such as the Wedge-tailed Shearwater (*Puffinus pacificus*), are even able to construct nest burrows in the sandy soil, but only on islands where plant roots are sufficient to hold the soil in place. While some seabirds use specific plant species, others are more general in preference. Bird species that nest in bushes and trees generally use particular plant species; those nesting on the ground are less specific. Thus the different kinds of vascular plant species on a low, sandy island are important to breeding seabirds.

Besides breeding and potentially breeding seabirds, the total number of bird species is composed of migrant shorebirds and vagrant or accidental seabird and freshwater species. The shorebirds depend indirectly on plants for food; most feed on insects, small marine invertebrates, and occasionally bird eggs. Available information indicates that vagrant and accidental species of gulls usually do not starve; appropriate food resources and fresh water are present (Sibley and McFarlane 1968).

Area of the island was the second most important ecological variable for SEAB (5.7% of variance), SEAT (8.6%), and BIRDS (9.2%). Since seabirds are colonial breeders, it is not surprising that area is also important, for as island area increases, species richness and population numbers can also increase. During the peak breeding period, it is common for an island to be almost completely covered by nesting birds, especially Sooty Terns.

Thus, there is indeed a similarity between ecological variables and plant and bird species richness on high, rocky islands and on low, sandy islands. On both, number of plant species account chiefly for number of birds species, while, in turn, some form of island area accounts for number of plant species. Differences between the two island types lie in secondary factors. For land birds on high, rocky islands isolation was the secondary factor, while for seabirds on low, sandy islands area was the secondary factor.

Seabirds, however, utilize islands differently than do land birds. The former are pelagic, depending entirely upon the ocean for a source of food and

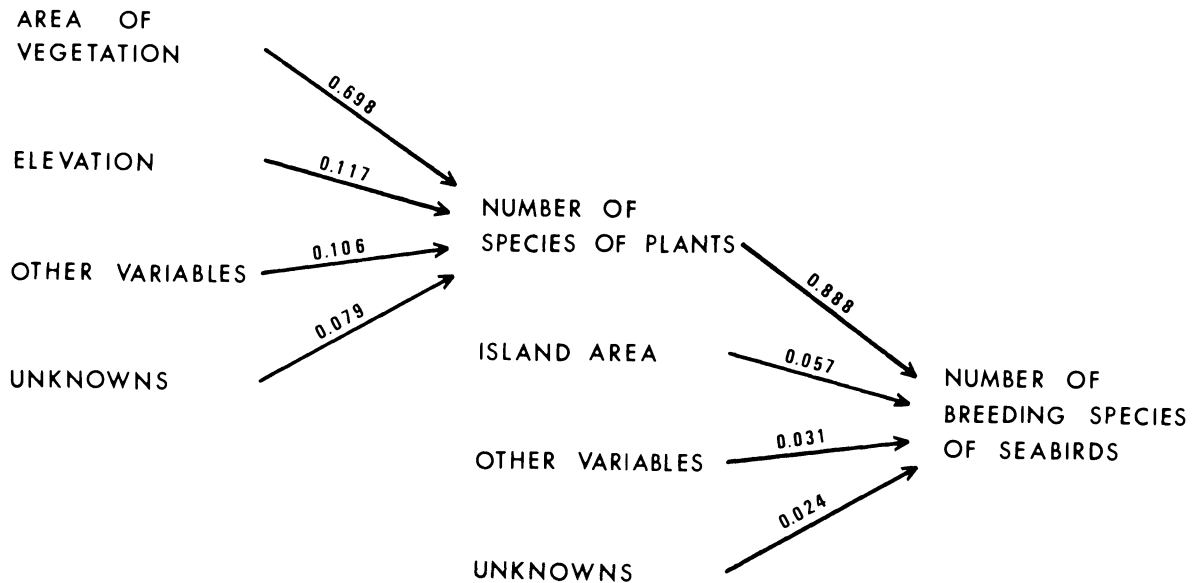


FIG. 2. Path diagram showing relationships among selected ecological variables and number of species of breeding seabirds on low, sandy, oceanic islands as indicated by stepwise linear regression. Numbers given are increases in the coefficient of multiple determination ( $R^2$ ) when the variable is added in the regression equation; they are an estimation of the relative contribution of each independent variable toward explaining numbers of plant and bird species.

water. Many species travel long distances in search of food, and most can alight on the ocean surface for long durations; others are able to stay aloft for long periods. Seabirds use islands principally for nesting and roosting during their breeding months; many species are pelagic for the rest of the year and actually avoid islands.

Seabirds at Pearl and Hermes Reef and French Frigate Shoals have a choice of 9 and 13 islands within their respective reefs upon which to nest or roost. Although each species may have different feeding adaptations, and competition may occur, food in the surrounding ocean areas has been available in most recent years for production of reasonable numbers of offspring (Amerson 1971, Amerson et al., *in press*). If food regulated island selection, all islands within the reef would have similar numbers of species. Such is not the case. As Ashmole (1963) has pointed out, however, food is of prime importance in regulation of population numbers of tropical oceanic birds.

As this study shows, island ecological diversity, and specifically number of plant species, is of prime importance in regulating use of low, sandy, oceanic islands as breeding areas by species of seabirds.

I have constructed a simple path diagram for numbers of breeding seabird species on low, sandy islands (Fig. 2) similar to that of Power (1972:457) for numbers of land bird species. About 89% of the variation in numbers of breeding seabird species

is explained by variation in the numbers of vascular plant species. An additional 6% of the variation is accounted for by island area, while 3% is attributed to all other variables; only 2% is from unknown factors. In turn, 70% of the variation in numbers of plant species is explained by area of vegetation, 12% by elevation, 11% by all other variables, and 7% by unknown factors.

Examination of this simple path diagram enables one to better understand the relationships between island ecological variables and species of vascular plants and breeding seabirds. Knowledge of basic island ecological variables and the use of multiple stepwise regression, from which the path diagram was developed, make it possible to predict species richness on oceanic islands (Table 1). Because many of these islands are inaccessible and thus expensive (and at times hazardous) to survey regularly, such a tool, used in conjunction with aerial or satellite photography and periodic surveys, would enable island biologists and, in the case of the northwestern Hawaiian Islands, Refuge administrators to oversee seasonal ecological and species changes.

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APPENDIX I. Status of bird species on 18 low, sandy, nondisturbed islands of the northwestern Hawaiian Islands (adapted from Amerson 1971, Amerson et al., *in press*)<sup>a</sup>

Species	French Frigate Shoals										Pearl and Hermes Reef							
	BARE	BGIN	DISA	LGIN	MULL	NEAR	ROUN	SHAR	TRIG	WHSK	BIRD	GRAS	KITT	LNOR	NORT	PLAN	SAND	SEAL
<i>Diomedea nigripes</i>		B <sup>b</sup>	B	B			B		B	B	B	B	B	B				B
<i>D. immutabilis</i>		B							B	B	B	B	B	B				B
<i>Pterodroma hypoleuca</i>												B			B			B
<i>Bulweria bulwerii</i>									P	B								
<i>Puffinus griseus</i>										A								
<i>P. pacificus</i>				B			B		B	B		B			B			B
<i>P. nativitatis</i>									B	P				P				
<i>Oceanodroma tristrami</i>										B		P		B				B
<i>Phaethon rubricauda</i>									B	B		B	P	B				B
<i>Sula dactylatra</i>		B	P	B			B	P	B	B	B	B	B	B	P	P	P	B
<i>S. sula</i>									B	B	B	B	B	B				P
<i>S. leucogaster</i>			P	P			P	P	P	B		P	P		P			P
<i>Fregata minor</i>			P	P			P	P	P	B		B	P		B			B
<i>Anas acuta</i>									A									
<i>Puffinus dominica</i>		P		P			P		P	P		P	P	P	P			P
<i>Numenius tahitiensis</i>									P	P		P		P				P
<i>Heteroscelus incanum</i>			P						P	P		P	P	P				P
<i>Arenaria interpres</i>		P	P	P			P		P	P	P	P	P	P	P	P	P	P
<i>Crocethia alba</i>			P				P		P	P		P	P	P				P
<i>Larus delawarensis</i>									A	A				A				
<i>L. argentatus</i>													A					
<i>L. glaucescens</i>									A					A	A			A
<i>Rissa tridactyla</i>																		
<i>Sterna lunata</i>			P						B	B	P	B	P		P			B
<i>S. fuscata</i>									B	B		P		P				B
<i>Anous stolidus</i>	P	P	P	B	P	P	B	P	B	B		B	P	B		P	P	B
<i>A. tenuirostris</i>		P	P	P	P		P	P	P	P		B		B	P			B
<i>Gygis alba</i>									P	P		P		P				P
<i>Fratercula corniculata</i>	—	—	—	—	—	—	—	—	—	—	—	A	—	A	—	—	—	—
Totals																		
SEAB <sup>c</sup>	0	3	1	4	0	0	4	0	10	13	3	11	3	3	11	0	0	12
SEAT	1	5	7	7	2	1	7	5	15	16	5	15	7	6	16	2	3	15
BIRDS	1	7	10	9	2	1	10	5	23	23	7	22	12	12	23	3	4	21

<sup>a</sup> Excluding natural dispersal of known human introductions from nearby disturbed islands; Table 1 gives island names.

<sup>b</sup> B = Breeding; P = Present; A = Accidental.

<sup>c</sup> SEAB = breeding species of seabirds; SEAT = total (breeding + potential breeding) species of seabirds; BIRDS = total species of birds.

(See APPENDIX II, next page)

APPENDIX II. Status of plant species on 18 low, sandy, nondisturbed islands of the northwestern Hawaiian Islands (adapted from Amerson 1971, Amerson et al., *in press*)<sup>a</sup>

Species	French Frigate Shoals										Pearl and Hermes Reef							
	BARE	BGIN	DISA	LGIN	MULL	NEAR	ROUN	SHAR	TRIG	WHSK	BIRD	GRAS	KITT	LNOR	NORT	PLAN	SAND	SEAL
<i>Cenchrus echinatus</i>									A <sup>b, c</sup>									
<i>Eragrostis variabilis</i>											Z			Z				Z
<i>Lepturus repens</i>				N			N		Z	Z		Z		Z	Z			Z
<i>Setaria vericellata</i>									A	A		A						
<i>Chenopodium oahuensis</i>									Z	Z								
<i>Achyranthes splendens</i>												Z			Z			Z
<i>Boerhavia repens</i>				N			N	N	Z	Z		Z		Z	Z			Z
<i>Sesuvium portulacastrum</i>																		Z
<i>Portulaca lutea</i>		N		N			N		Z	Z					Z			Z
<i>Capparis sandwichiana</i>																		N
<i>Brassica campestris</i>															A			
<i>Lepidium bidentatum</i>												Z			Z			Z
<i>Tribulus cistoides</i>							N		Z	Z		Z		Z	Z			Z
<i>Tournefortia argentea</i>									Z	Z		Z		Z	Z			Z
<i>Solanum nelsoni</i>												Z			Z			Z
<i>S. nigrum</i>												Z						
<i>Sicyos caumii</i>															Z			Z
<i>Scaevola taccada</i>									Z	Z		Z			Z			Z
PLS <sup>d</sup>	0	1	0	3	0	0	4	1	9	8	0	11	0	4	12	0	0	11

<sup>a</sup> Table 1 gives island names.  
<sup>b</sup> Eliminated in late 1969.  
<sup>c</sup> A = adventive, N = native.  
<sup>d</sup> Total species of plants.