

ANNUAL VARIABILITY IN THE ABUNDANCE OF MIGRANT LANDBIRDS ON SOUTHEAST FARALLON ISLAND, CALIFORNIA

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ABSTRACT.—I analyzed the occurrences of 217 species of migrant landbirds on Southeast Farallon Island, 43 km west of San Francisco, California, from 10 yr of daily censuses, fall 1968 to spring 1978. I divided species into 12 subgroups to reflect seasonal and geographical distributions on the mainland. The abundances of the various subgroups on the Farallones, in both fall and spring, were directly related to the proximity to the island of their breeding and wintering ranges and normal migration routes. For most subgroups, abundances were greater in fall than in spring. The great majority of fall individuals were hatching-year birds, and I suspect that many, if not most, spring individuals were second-year birds. Highly significant year-to-year variations occurred in the number of individuals that arrived on the Farallones and in the proportion of individuals in the various subgroups, despite the fact that the number of species and proportion of species in the various subgroups remained statistically invariant from year to year. Of particular interest were 5 fall days and 4 spring days when exceptional numbers of birds arrived on the island. These wave days were probably the result of local weather conditions near the Farallones. The numbers of individuals of most subgroups of wintering and summering species, especially coastal subgroups, increased significantly on wave days, but the numbers of vagrants did not. The annual variations in abundance of Farallon landbirds were probably caused by variations in the number of young produced each summer, by long-range weather patterns acting over large areas of the continent, and by variations in local weather conditions. Vagrant species significantly increased in abundance in both fall and spring during the second 5 yr of this study. I suggest that this could be caused by a selective increase in the proportion of dispersing individuals (including vagrants) in populations subjected to increased rates of habitat change. *Received 17 February 1982, resubmitted 7 June 1983, accepted 6 July 1983.*

OBSERVATIONS of grounded migrants have long constituted a major methodology for studying bird migration. Such studies, however, have usually provided only qualitative descriptions of species composition, relative abundance, and timing of migration at certain locations. Lack of accurate quantitative data stems from difficulties inherent in the following: (1) obtaining consistent census coverage free of observer bias; (2) conducting censuses in heavily vegetated habitats; (3) eliminating habitat preference biases among the species studied; and (4) monitoring the daily turnover rates, that is, distinguishing newly arrived individuals from those that arrived earlier.

Banding studies, to some extent, have been successful in overcoming these difficulties, especially with regard to daily turnover rates (MacArthur and MacArthur 1974, Manly 1977, Hussell 1981, Karr 1981). These studies, however, suffer from biases introduced by netting and trapping, including the effects on capture rates of weather (Stewart 1971), baiting, and

species-specific behavioral characteristics (flocking, foraging height, home-range size, and food preferences). In addition, both banding and census techniques generally fail to distinguish transient individuals from locally dispersing ones.

Southeast Farallon Island, located 43 km west of San Francisco, California, provides a nearly ideal situation for monitoring the occurrences of grounded migrants. Because of the island's small size (about 36 ha) and its open terrain, daily censuses of virtually all landbirds present can be obtained. Most of the sampling biases described above are eliminated, and habitat biases are minimized, because only poor habitat is available for all but a few open-country species. Furthermore, the opportunistic operation of a few nets and traps can supply sufficient information to estimate daily turnover rates accurately. Finally, because the island lies 32 km from the nearest mainland location, the only individuals to occur there are migrants (DeSante and Ainley 1980). As a result, the

abundance and annual variability of all migrants can be quantitatively analyzed in detail.

Southeast Farallon is also ideal because it attracts migrants from a wide range of geographical locations. A total of 218 landbird species, which originated from throughout North America, was documented as of 2 October 1979 (DeSante and Ainley 1980). The Farallones, therefore, can provide comparative data on the patterns of abundance and variability shown by landbirds that originate from or are bound for widely different geographical areas. Detailed quantitative studies of grounded migrants are needed to complement radar studies, such as those reviewed by Richardson (1978), if a comprehensive understanding of migration *in situ* is to be developed. Gauthreaux (1979) has also stressed the need for obtaining comparative data on bird migration.

The objectives of this study are: (1) to describe quantitatively the species composition and abundance of migrant landbirds on the Farallones as a function of their seasonal and geographical distribution on the mainland; (2) to describe quantitatively their annual variations in abundance; (3) to investigate the relationship between their annual variability and abundance; and (4) to provide quantitative information regarding long-term changes in abundance. In meeting these objectives, I provide information on the origins of migrant individuals on the Farallones, information on the predictability and the degree of synchronization of their annual variations, clues to the possible causes of their annual variations, and clues to the possible influences of both local and long-range weather on their occurrences.

LOCATION

The South Farallon Islands are located at the edge of the continental shelf (37°42'N, 123°00'W). The nearest mainland locations are Point Reyes and Bolinas Point, 32 km north and northeast, respectively. The South Farallones consist of two major islands, Southeast Farallon and West End, and several large nearby rocks, in all an area of less than 50 ha. DeSante and Ainley (1980) provided a general description of the islands and included references covering their geology, topography, edaphic conditions, weather, vegetation, and history.

The vast majority of landbirds that reach the Farallones concentrate on Southeast Farallon, particularly around the three trees, the few buildings and water tanks, the lighthouse, the top and south slope of Lighthouse Hill, the grassy marine terrace, and the

two surge channels at the leeward (east) end of the island. These areas are readily accessible for censusing throughout the year. Thus, all census data reported herein are limited to Southeast Farallon.

METHODS

Censuses of landbirds and nonbreeding waterbirds on Southeast Farallon have been conducted daily (weather permitting) by the Point Reyes Bird Observatory (PRBO) since 3 April 1968. Because the early spring of 1968 was not covered and a few early spring migrants were undoubtedly missed, all spring 1968 data have been excluded. Included are daily censuses of landbirds for 10 falls (1968-1977) and 10 springs (1969-1978).

One or more experienced observers conducted censuses, primarily in the morning, by opportunistically visiting all accessible areas. An effort was made to identify and count all individuals present. In addition, all personnel remained on the lookout for landbirds throughout the day. Each evening they participated in writing the Farallon Journal, in which all species were entered along with the best combined group estimate of their numbers and all pertinent age, sex, plumage, and banding information.

On most days, mist nets and traps were used to capture landbirds. Two permanent 12-m nets were stacked, one above the other, adjacent to the two cypress trees, and one or more portable nets were occasionally placed elsewhere. A permanent water-baited funnel-type "house" trap was located beneath the cypress trees, and a Heligoland trap surrounded the remaining tree, a prostrate pine. Banding provided invaluable data on the daily turnover of individual birds. It also provided for the in-hand determination of species that are difficult to identify, such as *Empidonax* flycatchers and certain wood warblers in immature plumage. Criteria for the acceptance of sight records were outlined in DeSante and Ainley (1980).

The vast majority of visitant landbirds appeared during fall, roughly late July to early December, and spring, roughly early March to late June. The separations of occurrences between fall and winter, winter and spring, and spring and fall were based on guidelines detailed in DeSante and Ainley (1980). Only spring and fall occurrences are treated in this paper. Winter resident individuals that arrived during the fall were not included among the fall occurrences.

Abundance is defined as the total number of individuals that occurred in a given season (fall or spring) during the entire 10-yr period. The algorithm used to determine this total was described by DeSante and Ainley (1980).

A total of 214 of the 218 landbird species documented from the Farallones as of 2 October 1979 (DeSante and Ainley 1980) was recorded during the 10 yr considered here. The Starling (*Sturnus vulgaris*)

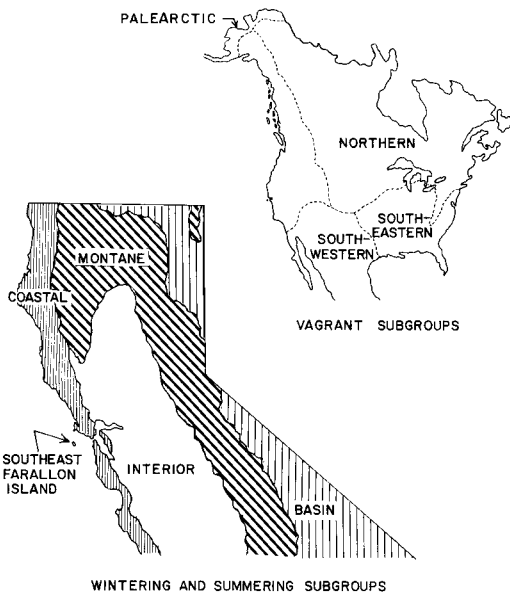


Fig. 1. Map of northern California (and North America: inset) showing the proximity of Southeast Farallon Island to the geographical regions that characterize the various subgroups.

was excluded from this study, because its recent dramatic population increase as a breeding, wintering, and migrant species on the Farallones (apparently a result of its continuing population explosion on the adjacent mainland) precludes a meaningful assessment of any intrinsic annual variability in its occurrence rate. Furthermore, it has become the most abundant fall migrant landbird on the Farallones and thus would seriously bias the annual variability of any group of species with which it was included.

Four of the remaining 213 species occurring on the Farallones during the 10 yr of this study contain two distinct forms, which are easily identified in the field and which originate from different parts of the continent. These were treated separately, bringing the number of taxa to 217. These species are Common Flicker (*Colaptes auratus*; "Yellow-shafted" and "Red-shafted"), Yellow-rumped Warbler (*Dendroica coronata*; "Myrtle" and "Audubon's"), Northern Oriole (*Icterus galbula*; "Baltimore" and "Bullock's"), and Dark-eyed Junco (*Junco hyemalis*; "Slate-colored" and "Oregon").

The 217 taxa were classified into three groups according to the seasonality of their occurrences in central California (roughly 38°N). First are the **wintering species**, which occur there in maximum numbers during winter, although many also breed in lesser numbers. Second are the **summering species**, which occur in maximum numbers during summer, although several winter regularly in reduced numbers. Third are the **vagrant species**, which occur in maxi-

TABLE 1. Frequency distributions of three independent indices used to develop a commonness index or estimate of the total population size for the various Farallon species (see text).

Rank	Number of species given that rank		
	Range	Frequency	Abundance
1	8	21	4
2	41	133	26
3	74	51	64
4	55	12	99
5	39	—	24
Total	217	217	217
Mean	3.35	2.25	3.52

imum numbers as fall and/or spring transients; their breeding and wintering ranges and migration routes do not encompass central California. These latter are basically misdirected, out-of-range migrants.

Each of these groups was further divided into four subgroups that reflect the proximity of their normal ranges to the Farallones. The geographical regions that characterize these subgroups were described by DeSante and Ainley (1980) and are shown in Fig. 1. The subgroups for both the wintering and summering groups are the same: **coastal**, **interior**, **montane**, and **basin**. The four vagrant subgroups include **northern**, **southeastern**, **southwestern**, and **palearctic** species.

The classification of the 217 taxa into these 12 subgroups followed DeSante and Ainley (1980), with several exceptions. All species classified into the resident coastal and resident interior classes of DeSante and Ainley (1980) were placed in the coastal wintering and interior wintering subgroups, respectively, except Rock Dove (*Columba livea*), Mourning Dove (*Zenaidura macroura*), Common Yellowthroat (*Geothlypis trichas*), House Sparrow (*Passer domesticus*), House Finch (*Carpodacus mexicanus*), American Goldfinch (*Carduelis tristis*), and Lesser Goldfinch (*Carduelis psaltria*), which were placed in the coastal summering subclass, and Mockingbird (*Mimus polyglottus*), Phainopepla (*Phainopepla nitens*), and Sage Sparrow (*Amphispiza belli*), which were placed in the interior summering subclass. The six landbird species added to the Farallon list between 3 April 1976 and 31 July 1978 [unclassified in DeSante and Ainley (1980)] were placed as follows: Bald Eagle (*Haliaeetus leucocephalus*), coastal wintering; Black-chinned Hummingbird (*Archilochus alexandri*), interior summering; Yellow-bellied Flycatcher (*Empidonax flaviventris*), northern vagrant; and Lucy's Warbler (*Vermivora luciae*), Scott's Oriole (*Icterus perisorum*), and Hepatic Tanager (*Piranga flava*), southwestern vagrant.

In order to determine whether or not the abundance of the various species on the Farallones was related to the size of their source populations, it was necessary to develop commonness indices (estimates

TABLE 2. Number of *species* of migrant landbirds recorded on Southeast Farallon Island.

Species group*	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	10-yr mean	10-yr total	10-yr spring and fall total
A. Fall													
Wintering													
Coastal	38	38	40	37	42	42	42	44	42	41	40.6	53	54
Interior	5	4	4	4	5	6	5	4	4	5	4.6	9	9
Montane	1	0	0	0	4	1	0	0	1	2	0.9	5	5
Basin	3	0	2	3	2	2	2	1	1	2	1.8	4	4
Total	47	42	46	44	53	51	49	49	48	50	47.9	71	72
Summering													
Coastal	23	19	21	22	23	22	23	23	17	19	21.2	27	27
Interior	11	8	10	10	15	12	13	9	10	11	10.9	20	22
Montane	9	11	11	11	13	12	12	12	9	13	11.3	15	16
Basin	4	2	4	3	5	2	4	3	4	2	3.3	6	6
Total	47	40	46	46	56	48	52	47	40	45	46.7	68	71
Vagrant													
Northern	22	22	21	19	29	23	33	28	24	26	24.7	42	42
Southeastern	4	3	1	2	2	2	8	6	3	5	3.6	13	20
Southwestern	1	2	2	2	0	3	0	1	3	2	1.6	7	9
Paleartic	1	0	0	0	0	0	1	0	0	0	0.2	2	3
Total	28	27	24	23	31	28	42	35	30	33	30.1	64	74
Grand total	122	109	116	113	140	127	143	131	118	128	124.7	203	217
Species group*	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	10-yr mean	10-yr total	
B. Spring													
Wintering													
Coastal	23	26	28	18	31	27	28	28	25	32	26.6	40	
Interior	1	1	0	0	2	2	2	1	3	2	1.4	5	
Montane	0	1	0	0	1	1	0	0	0	1	0.4	3	
Basin	1	0	1	1	0	0	1	1	1	2	0.8	2	
Total	25	28	29	19	34	30	31	30	29	37	29.2	50	
Summering													
Coastal	25	22	17	19	19	23	26	21	25	24	22.1	27	
Interior	11	10	7	6	9	7	11	4	11	10	8.6	16	
Montane	12	12	12	12	9	10	10	11	13	8	10.9	16	
Basin	1	3	1	0	2	3	3	2	4	3	2.2	6	
Total	49	47	37	37	39	43	50	38	53	45	43.8	65	
Vagrant													
Northern	20	15	10	15	19	14	25	12	18	15	16.3	35	
Southeastern	10	4	2	4	3	4	6	3	3	5	4.4	14	
Southwestern	1	1	0	0	1	0	1	0	1	0	0.5	3	
Paleartic	0	0	1	0	0	0	0	0	0	0	0.1	1	
Total	31	20	13	19	23	18	32	15	22	20	21.3	53	
Grand total	105	95	79	75	96	91	113	83	104	102	94.3	168	

* Classified according to their seasonal and geographical distribution in mainland California (see text).

of the total population sizes) for each of the 217 taxa. These commonness indices were obtained as the product of three independent rank indices: the geographical size of the species' breeding range, the frequency of occurrence or amount of suitable breeding habitat within the breeding range, and the numerical

breeding abundance within suitable breeding habitat. Range was ranked from 1 (very small, e.g. Golden-cheeked Warbler, *Dendroica chrysoparia*) to 5 (very extensive, e.g. Great Horned Owl, *Bubo virginianus*). Frequency was ranked from 1 (very locally distributed, e.g. Marsh Wren, *Cistothorus palustris*) to 4 (near-

TABLE 3. Differences between fall and spring in the number of species that occurred on the Farallones as determined by Mann-Whitney U -tests.

Species group ^a	Mean number of species/year		$U_{s(10,10)}$ ^b	P ^c
	Fall	Spring		
Wintering				
Coastal	40.6	26.6	100.0	<0.001
Interior	4.6	1.4	100.0	<0.001
Montane	0.9	0.4	59.0	>0.2
Basin	1.8	0.8	86.0	<0.01
Total	47.9	29.2	100.0	<0.001
Summering				
Coastal	21.2	22.1	61.0	>0.2
Interior	10.9	8.6	73.5	<0.1
Montane	11.3	10.9	56.5	>0.2
Basin	3.3	2.2	74.0	<0.1
Total	46.7	43.8	64.5	>0.2
Vagrant				
Northern	24.7	16.3	92.5	<0.002
Southeastern	3.6	4.4	63.0	>0.2
Southwestern	1.6	0.5	80.0	<0.05
Palearctic	0.2	0.1	55.0	>0.2
Total	30.1	21.3	86.0	<0.01
Grand total	124.7	94.3	98.5	<0.002

^a Classified according to their seasonal and geographical distribution in mainland California (see text).

^b Mann-Whitney statistic.

^c Probability for two-tailed test.

ly ubiquitously distributed, e.g. American Robin, *Turdus migratorius*). Abundance was ranked from 1 (rare, e.g. Peregrine Falcon, *Falco peregrinus*) to 5 (abundant, e.g. Red-winged Blackbird, *Agelaius phoeniceus*). The product of these three indices thus produced a commonness index that could range from 1 (a rare, very locally distributed species with a very small range) to 100 (an abundant, nearly ubiquitously distributed species with a very extensive range). The mean commonness index for all 217 species was 28.2. The frequency distributions for each of the three individual indices are presented for the 217 species in Table 1.

The following statistical tests were employed in this paper. The Wilcoxon matched-pairs signed-ranks test was used to compare the differences in (a) the number of species, (b) the proportion of the total number of species, (c) the number of individuals, or (d) the number of individuals/species that occurred between any two groups or subgroups of species in either fall or spring over the 10 yr. This test was also used to compare the differences that occurred between the first 5 and second 5 yr of the study in the number of individuals of each species in a given group or subgroup. In all cases, the Wilcoxon rank sum statistic is given as T_s . Mann-Whitney U -tests

were used to compare differences in commonness indices between any two groups or subgroups of species. They were also used to compare differences between fall and spring in the number of species or individuals of any group or subgroup that occurred on the Farallones and to compare differences between wave days and nonwave days in the number of individuals that occurred. If the number of samples in any one group or subgroup was greater than 20, the Mann-Whitney statistic, $U_{s(n_1, n_2)}$, was given at $t_{s(20)}$. Spearman Rank Correlation Coefficients (r_s) were calculated and used to investigate the relationships between fall and spring Farallon abundance, and between Farallon abundance in either fall or spring and commonness of each of the species in any group or subgroup. They were also used to investigate the relationship between the number of individuals of a given group or subgroup that arrived in a given fall and the number that arrived the following spring and vice versa. Finally, the differences between distributions were tested by the Chi-square statistic. Unless stated to the contrary, probability values in all cases are given for two-tailed tests.

RESULTS

SPECIES COMPOSITION

The number of species in each of the 12 subgroups that occurred during each of the 10 yr is presented, along with the total number of species that occurred during the entire 10-yr period, in Table 2A (fall) and 2B (spring). No significant difference occurred between the total number of wintering and summering species in fall, but summering species outnumbered wintering species in spring (Wilcoxon matched-pairs signed-ranks test: $T_s = 0$, $n = 10$, $P < 0.01$). The numbers of vagrant species were significantly less than the numbers of both wintering species ($T_s = 0$, $n = 10$, $P < 0.01$ in fall; $T_s = -3.0$, $n = 9$, $P < 0.02$ in spring) and summering species ($T_s = 0$, $n = 10$, $P < 0.01$ in both fall and spring).

The proportion, p , of the total number of fall vagrant species that occurred each fall ($\bar{p} = 0.470$) was significantly less than those same proportions for both wintering species ($\bar{p} = 0.675$; $T_s = 0$, $n = 10$, $P < 0.01$) and summering species ($\bar{p} = 0.687$; $T_s = 0$, $n = 10$, $P < 0.01$). Likewise, the proportion of the total number of spring vagrant species that occurred each spring ($\bar{p} = 0.402$) was also significantly less than those same proportions for both wintering species ($\bar{p} = 0.580$; $T_s = -3.0$, $n = 10$, $P < 0.01$) and summering species ($\bar{p} = 0.674$; $T_s = 0$,

$n = 10$, $P < 0.01$). This was because a greater proportion of the vagrant species were very rare and did not occur every year (see below). The differences in these proportions between wintering and summering species were not significant, however, in either fall or spring.

Significantly more total species occurred in fall than in spring (Table 3). This same result also held for total wintering species and for total vagrant species (but not for total summering species), as well as for five of the individual subgroups (coastal, interior, and basin wintering and northern and southwestern vagrant species). In contrast, more coastal summering species and southeastern vagrant species occurred in spring than in fall, but the differences were not significant.

ANNUAL VARIATION IN SPECIES COMPOSITION

Table 2 indicates that relatively little year-to-year variation existed in either fall or spring in the number of species in any subgroup that occurred on the Farallones. In fact, the hypothesis that the mean number of total species (124.7 in fall, 94.3 in spring) was invariant over the 10 yr could not be rejected for either season ($\chi^2 = 9.111$, $df = 9$, $P > 0.1$ in fall; $\chi^2 = 14.487$, $df = 9$, $P > 0.1$ in spring). This same result also held true for the total wintering, summering, and vagrant groups in both fall and spring ($\chi^2 \leq 9.332$, $df = 9$, $P > 0.1$ for all cases except total vagrants in spring, for which $\chi^2 = 15.967$, $df = 9$, $P > 0.05$), and for all five of the subgroups, for which the mean (expected) value was greater than 5.0 (coastal wintering, coastal, interior, and montane summering; and northern vagrant) in both fall and spring ($\chi^2 \leq 10.313$, $df = 9$, $P > 0.1$ for all cases). The Farallones, therefore, drew a statistically constant number of species each year.

Not only did the number of species remain constant from year to year, the relative proportions of wintering, summering, and vagrant species also remained invariant over the 10 yr in both fall ($\chi^2 = 6.522$, $df = 18$, $P > 0.9$) and spring ($\chi^2 = 15.485$, $df = 18$, $P > 0.5$). Moreover, among summering species, the relative proportions of coastal, interior, and montane species (those with a mean number of species greater than 5.0) also remained invariant over the 10 yr ($\chi^2 = 2.846$, $df = 18$, $P > 0.99$ in fall; $\chi^2 = 7.062$, $df = 18$, $P > 0.95$ in spring). The

species composition on the Farallones, therefore, was statistically constant from year to year.

ABUNDANCE

The number of individuals in each of the 12 subgroups that occurred on Southeast Farallon Island during each of the 10 yr is presented in Table 4A (fall) and 4B (spring). The mean abundance (in terms of individuals/species) of each of the 12 subgroups for each of the 10 yr is presented in Table 5A (fall) and 5B (spring). A summary of these data, along with the mean commonness index (an estimate of the total population size of the species), is given for each of the 12 subgroups in both fall and spring in Table 6. The mean abundances of the subgroups were not significantly correlated with their mean commonness indices in either fall (Spearman rank correlation: $r_s = 0.566$, $df = 10$, $P > 0.05$) or spring ($r_s = 0.559$, $df = 10$, $P > 0.05$). Even within subgroups, Farallon abundances of individual species were generally only weakly (if at all) correlated with commonness indices in either fall or spring (Table 7), although there were exceptions where strong correlation was obtained (basin wintering, and interior and basin summering). On average, commonness accounted for only about 28% of the variation in abundance in either season. Clearly then, other factors in addition to total population size must operate to determine the abundance of the various migrant landbird species on the Farallones. A detailed numerical analysis of these factors will be the subject of a future paper. A few comments, however, are in order, as they pertain to this paper.

Abundance in fall.—Significantly more individuals/species occurred in fall for wintering species (418.5) than for either summering species (101.3; Wilcoxon's matched-pairs signed-ranks test: $T_s = 0$, $n = 10$, $P < 0.01$) or vagrant species (20.9; $T_s = 0$, $n = 10$, $P < 0.01$). Wintering species, in fact, accounted for 77.5% of the total fall individuals (Table 6). This is of special importance, because the mean commonness indices did not differ significantly between wintering, summering, and vagrant species (Mann-Whitney U -tests: $t_{[0.05]} \leq 1.333$, $P > 0.1$ for all three cases).

The vast majority of the Farallon individuals of wintering species were coastal wintering species, which alone accounted for 76.6% of all

TABLE 4. Number of individuals of migrant landbirds recorded on Southeast Farallon Island.^a

Species group ^b	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	Total	CV ^c
A. Fall												
Wintering												
Coastal	3,917 (1,340)	2,591 (1,471)	3,483 (2,309)	1,264	12,333 (2,090)	1,146	1,856	936	1,413	827	29,766 (14,652)	116.2 (33.0)
Interior	33	14	18	19	38	41	42	16	21	26	268	40.3
Montane	1	0	0	0	8	1	0	0	1	3	14	178.8
Basin	(1)	(0)	(0)	(0)	(6)	(6)					(12)	(161.0)
Total	3,958 (1,381)	2,605 (1,485)	3,509 (2,335)	1,298	12,388 (2,143)	1,196	1,924	956	1,437	859	30,130 (15,014)	115.0 (32.5)
Summering												
Coastal	449 (429)	225 (215)	401 (393)	433	601 (563)	457	626	636	339	364	4,531 (4,455)	29.6 (29.7)
Interior	110	37	71	53	88	130	119	68	59	61	796	38.8
Montane	209	134	153	139	272	155	283	159	86	190	1,780	34.7
Basin	(196)	(132)	(152)	(152)	(186)						(1,678)	(30.9)
Total	6 (6)	3 (3)	7 (7)	6	15 (13)	3	27	4	6	6	83 (81)	89.1 (89.1)
Total	774 (741)	399 (387)	632 (623)	631	976 (850)	745	1,055	867	490	621	7,190 (7,010)	28.7 (27.7)
Vagrant												
Northern	106	91	68	89	176	93	342	228	127	156	1,476	56.8
Southeastern	4	3	2	2	10	2	11	7	6	8	55	62.0
Southwestern	1	2	2	2	0	4	0	1	3	2	17	73.6
Palearctic	1	0	0	0	0	0	1	0	0	0	2	210.8
Total	112	96	72	93	186	99	354	236	136	166	1,550	55.6
Grand total	4,844 (2,234)	3,100 (1,968)	4,213 (3,030)	2,022	13,550 (3,179)	2,040	3,333	2,059	2,063	1,646	38,870 (23,574)	91.5 (25.1)

TABLE 4. Continued.

Species group ^b	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	Total	CV ^c
B. Spring												
Wintering												
Coastal	553 (450)	224	972 (620)	125	1,057 (450)	377	301	234	292	391	4,526 (3,464)	70.3 (40.9)
Interior	1	1	0	0	4	2	3	1	5	3	20	85.0
Montane	0	1	0	0	1	1	0	0	0	1	4	129.1
Basin	1	0	2	2	0	0	2	1	3	3	14	83.8
Total	555 (452)	226	974 (622)	127	1,062 (455)	380	306	236	300	398	4,564 (3,502)	69.7 (40.5)
Summering												
Coastal	1,298 (774)	559	966 (473)	310	250 (243)	303	524	211	241	291	4,953 (3,929)	73.4 (46.5)
Interior	45	45	27	9	23	14	45	8	18	23	257	56.9
Montane	154 (107)	52	124 (57)	39	43 (37)	35	58	38	69	59	671 (551)	59.6 (39.2)
Basin	8	9	5	0	11	3	11	3	21	6	77	76.7
Total	1,505 (926)	665	1,122 (554)	358	327 (312)	355	638	260	349	379	5,958 (4,796)	68.9 (43.9)
Vagrant												
Northern	57	43	12	40	35	49	141	27	98	42	544	69.5
Southeastern	11	7	2	9	6	4	18	7	7	6	77	56.8
Southwestern	1	1	0	0	1	0	1	0	1	0	5	105.4
Palearctic	0	0	1	0	0	0	0	0	0	0	1	316.2
Total	69	51	15	49	42	53	160	34	106	48	627	66.3
Grand total	2,129 (1,447)	942	2,111 (1,191)	534	1,431 (809)	788	1,104	530	755	825	11,149 (8,925)	53.1 (32.2)

^a Numbers in parentheses are after the removal of wave days (see text).
^b Classified according to their seasonal and geographical distribution in mainland California (see text).
^c Coefficient of variation = (100) × SD/mean.

TABLE 5. Mean abundance (number of individuals/species)^a of migrant landbirds on Southeast Farallon Island.^b

Species group ^c	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	Total
A. Fall											
Wintering											
Coastal	72.5 (24.8)	48.0 (27.2)	64.5 (42.8)	23.4	228.4 (38.7)	21.2	34.4	17.3	26.2	15.3	551.2 (271.3)
Interior	3.7	1.6	2.0	2.1	4.2	4.6	4.7	1.8	2.3	2.9	29.8
Montane	0.2 (0.2)	0.0 (0.0)	0.0 (0.0)	0.0	1.6 (1.2)	0.2	0.0	0.0	0.2	0.6	2.8 (2.4)
Basin	1.7	0.0	2.0	3.7	2.3	2.0	6.5	1.0	0.5	0.7	20.5
Total	55.0 (19.2)	36.2 (20.6)	48.7 (32.4)	18.0	172.1 (29.8)	16.6	26.7	13.3	20.0	11.9	418.5 (208.5)
Summering											
Coastal	16.6 (15.9)	8.3 (8.0)	14.9 (14.6)	16.0	22.3 (20.9)	16.9	23.2	23.6	12.6	13.5	167.8 (165.0)
Interior	5.0	1.7	3.2	2.4	4.0	5.9	5.4	3.1	2.7	2.8	36.2
Montane	13.1 (12.3)	8.4 (8.3)	9.6 (9.5)	8.7	17.0 (11.6)	9.7	17.7	9.9	5.4	11.9	111.3 (104.9)
Basin	1.0 (1.0)	0.5 (0.5)	1.2 (1.2)	1.0	2.5 (2.2)	0.5	4.5	0.7	1.0	1.0	13.8 (13.5)
Total	10.9 (10.4)	5.6 (5.5)	8.9 (8.8)	8.9	13.7 (12.0)	10.5	14.9	12.2	6.9	8.7	101.3 (98.7)
Vagrant											
Northern	2.5	2.2	1.6	2.2	4.2	2.2	8.1	5.4	3.0	3.7	35.1
Southeastern	0.2	0.1	0.1	0.1	0.5	0.1	0.5	0.3	0.3	0.4	2.7
Southwestern	0.1	0.2	0.2	0.2	0.0	0.4	0.0	0.1	0.3	0.2	1.9
Palearctic	0.3	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.7
Total	1.5	1.3	1.0	1.3	2.5	1.3	4.8	3.2	1.8	2.2	20.9
Grand total	22.3 (10.3)	14.3 (9.1)	19.4 (14.0)	9.3	62.4 (14.6)	9.4	15.4	9.5	9.5	7.6	179.1 (108.6)
Species group ^c	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	Total
B. Spring											
Wintering											
Coastal	10.2 (8.3)	4.1	18.0 (11.5)	2.3	19.6 (8.3)	7.0	5.6	4.3	5.4	7.2	83.8 (64.1)
Interior	0.1	0.1	0.0	0.0	0.4	0.2	0.3	0.1	0.6	0.3	2.2
Montane	0.0	0.2	0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.2	0.8
Basin	0.3	0.0	0.5	0.5	0.0	0.0	0.5	0.3	0.7	0.7	3.5
Total	7.7 (6.3)	3.1	13.5 (8.6)	1.8	14.7 (6.3)	5.3	4.3	3.3	4.2	5.5	63.4 (48.6)
Summering											
Coastal	48.1 (28.7)	20.7	35.8 (17.5)	11.5	9.3 (9.0)	11.2	19.4	7.8	8.9	10.8	183.4 (145.5)
Interior	2.0 (1.7)	2.0	1.2 (0.9)	0.4	1.0 (1.0)	0.6	2.0	0.4	0.8	1.0	11.7 (11.0)
Montane	9.6 (6.7)	3.3	7.7 (3.6)	2.4	2.7 (2.3)	2.2	3.6	2.4	4.3	3.7	41.9 (34.4)
Basin	1.3 (1.2)	1.5	0.8 (0.7)	0.0	1.8 (1.8)	0.5	1.8	0.5	3.5	1.0	12.8 (12.5)
Total	21.2 (13.0)	9.4	15.8 (7.8)	5.0	4.6 (4.4)	5.0	9.0	3.7	4.9	5.3	83.9 (67.5)
Vagrant											
Northern	1.4	1.0	0.3	1.0	0.8	1.2	3.4	0.6	2.3	1.0	13.0
Southeastern	0.5	0.3	0.1	0.5	0.3	0.2	0.9	0.3	0.3	0.3	3.9
Southwestern	0.1	0.1	0.0	0.0	0.1	0.0	0.1	0.0	0.1	0.0	0.6
Palearctic	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3
Total	0.9	0.7	0.2	0.7	0.6	0.7	2.2	0.5	1.4	0.6	8.5
Grand total	9.8 (6.7)	4.3	9.7 (5.5)	2.5	6.6 (3.7)	3.6	5.1	2.4	3.5	3.8	51.4 (41.1)

^a Total number of individuals that season divided by total number of species in both fall and spring.^b Numbers in parentheses are after removal of wave days (see text).^c Classified according to their seasonal and geographical distribution in mainland California (see text).

TABLE 6. Summary of the occurrences of migrant landbirds on Southeast Farallon Island during the 10 falls, 1968-1977, and 10 springs, 1969-1978.^a

Species group ^b	Total number of species ^c	Mean commonness index ^d	Fall			Spring		
			Total number of individuals	Percentage of total individuals	Individuals/species ^e	Total number of individuals	Percentage of total individuals	Individuals/species ^e
Wintering								
Coastal	54	33.6	29,766 (14,652)	76.6 (62.2)	551.2 (271.3)	4,526 (3,464)	40.6 (38.8)	83.8 (64.1)
Interior	9	18.8	268	0.7 (1.1)	29.8	20	0.2 (0.2)	2.2
Montane	5	17.6	14 (12)	<0.1 (0.1)	2.8 (2.4)	4	<0.1 (<0.1)	0.8
Basin	4	34.0	82	0.2 (0.3)	20.5	14	0.1 (0.2)	3.5
Total	72	30.7	30,130 (15,014)	77.5 (63.7)	418.5 (208.5)	4,564 (3,502)	40.9 (39.2)	63.4 (48.6)
Summering								
Coastal	27	43.0	4,531 (4,455)	11.7 (18.9)	167.8 (165.0)	4,953 (3,929)	44.4 (44.0)	183.4 (145.5)
Interior	22	20.4	796	2.0 (3.4)	36.2	257 (241)	2.3 (2.7)	11.7 (11.0)
Montane	16	22.6	1,780 (1,678)	4.6 (7.1)	111.3 (104.9)	671 (551)	6.0 (6.2)	41.9 (34.4)
Basin	6	18.7	83 (81)	0.2 (0.3)	13.8 (13.5)	77 (75)	0.7 (0.8)	12.8 (12.5)
Total	71	29.3	7,190 (7,010)	18.5 (29.7)	101.3 (98.7)	5,958 (4,796)	53.4 (53.7)	83.9 (67.5)
Vagrant								
Northern	42	27.9	1,476	3.8 (6.3)	35.1	544	4.9 (6.1)	13.0
Southeastern	20	21.8	55	0.1 (0.2)	2.7	77	0.7 (0.9)	3.9
Southwestern	9	15.6	17	<0.1 (0.1)	1.9	5	<0.1 (0.1)	0.6
Palaearctic	3	27.3	2	<0.1 (<0.1)	0.7	1	<0.1 (<0.1)	0.3
Total	74	24.7	1,550	4.0 (6.6)	20.9	627	5.6 (7.0)	8.5
Grand total	217	28.2	38,870 (23,574)	100.0 (100.0)	179.1 (108.6)	11,149 (8,925)	100.0 (100.0)	51.4 (41.1)

^a Numbers in parentheses are after the removal of wave days (see text).

^b Classified according to their seasonal and geographical distribution in mainland California (see text).

^c Ten-year fall and spring total.

^d An estimate of the total population size of the species obtained as the product of indices for range, frequency, and abundance (see text).

^e Total number of individuals that season divided by total number of species in both fall and spring.

fall migrants. They were thus significantly more abundant than all other subgroups of wintering species ($T_s = 0$, $n = 10$, $P < 0.01$ for all three cases). This is despite the fact that the mean commonness index did not differ significantly among any of the four subgroups (Mann-Whitney U -tests: $t_{s(\infty)} \leq 1.831$, $P > 0.05$ for all six cases). The great preponderance of coastal species in fall, however, was not unexpected. They are the only species whose "normal" fall

migrations, south or southwestward to the central California coast, bring large numbers directly toward the Farallones. Thus, they could reach the island without any misdirection, needing only to have overshoot the mainland by 30-45 min flight time or to have drifted but a few kilometers west of the coast.

The remaining three subgroups of wintering species combined accounted for less than 1% of the total fall individuals. Because interior and

TABLE 7. Spearman rank correlations (r_s) between Farallon abundance (total number of individuals over the entire 10 yr) and commonness index (an estimate of the total population size of the species; see text).^a

Species group ^b	Total number of species	Fall			Spring		
		r_s	$(r_s)^2$	P^c	r_s	$(r_s)^2$	P^c
Wintering							
Coastal	54	0.352 (0.380)	0.124 (0.144)	<0.01 (<0.01)	0.303 (0.298)	0.092 (0.089)	<0.05 (<0.05)
Interior	9	-0.125	0.016	—	0.121	0.015	—
Montane	5	-0.550 (-0.625)	0.303 (0.391)	— (—)	-0.625	0.391	—
Basin	4	0.950	0.903	—	0.750	0.563	—
Summering							
Coastal	27	0.363 (0.348)	0.132 (0.121)	<0.1 (<0.1)	0.452 (0.455)	0.204 (0.207)	<0.02 (<0.02)
Interior	22	0.692	0.479	<0.001	0.700 (0.680)	0.490 (0.462)	<0.001 (<0.001)
Montane	16	0.243 (0.249)	0.059 (0.062)	>0.1 (>0.1)	0.471 (0.490)	0.222 (0.241)	<0.1 (<0.1)
Basin	6	0.829 (0.829)	0.687 (0.687)	— (—)	0.371 (0.371)	0.138 (0.138)	— (—)
Vagrant							
Northern	42	0.384	0.147	<0.02	0.597	0.356	<0.001
Southeastern	20	0.131	0.017	>0.1	0.273	0.075	>0.1
Southwestern	9	0.279	0.078	—	0.317	0.100	—
Palaearctic	3	-0.625	0.391	—	0.875	0.766	—
Mean			0.278			0.284	

^a Numbers in parentheses are after the removal of wave days (see text).

^b Classified according to their seasonal and geographical distribution in mainland California (see text).

^c Probabilities are given only when sample size (total number of species) is greater than 10. Degrees of freedom = total number of species - 2.

basin species normally winter some distance inland from the California coast, most Farallon individuals of these species were probably somewhat misdirected. Basin wintering species, which would seem to need a greater degree of misdirection to reach the Farallones than interior wintering species, did tend to be less abundant than interior species ($T_s = -7.0$, $n = 9$, $P < 0.05$ one-tailed).

Montane wintering species were extremely scarce on the Farallones and were significantly less abundant than both interior and basin wintering species ($T_s = 0$, $n = 10$, $P < 0.01$ for both cases). Moreover, they were present only in half of the falls. These species, such as Clark's Nutcracker (*Nucifraga columbiana*), Evening Grosbeak (*Coccothraustes vespertinus*), and Red Crossbill (*Loxia curvirostra*), are typical winter irruption species that in many years never leave the mountains. Thus, their scarcity and sporadic nature on the Farallones are readily explained.

Summering species accounted for 18.5% of

the total fall migrants to the Farallones and, while significantly less abundant than wintering species, were significantly more abundant than vagrant species ($T_s = 0$, $n = 10$, $P < 0.01$). In general, summering species breed over various parts of western North America (and farther east in some species) and winter in Mexico or farther south. Because the western edge of the continent south of the Farallones veers strongly to the southeast, fall migrants of these species, at least from the western parts of their breeding ranges, must normally have pronounced easterly components to their southerly flights. Thus, most individuals that reached the Farallones in fall were probably at least slightly misdirected or wind-drifted westward. It is not surprising, therefore, that coastal wintering species, which need no misdirection to reach the Farallones in fall, were significantly more abundant than all four subgroups of summering species ($T_s \leq 3.0$, $n = 10$, $P < 0.01$ for all four cases).

Coastal species were the most numerous of

the summering species and were significantly more abundant than the other three subgroups ($T_s \leq 1.0$, $n = 10$, $P < 0.01$ for all cases). Large numbers of these species breed on the adjacent coast and, of the various summering subgroups, need the least misdirection to reach the Farallones. In addition, their mean commonness index was significantly greater than those indices for the other summering subgroups (Mann-Whitney U -tests: $t_{q[\infty]} \geq 2.955$, $P < 0.01$ for all three cases). No significant differences, however, were found among the mean commonness indices of the other three summering subgroups (Mann-Whitney U -tests: $t_{q[\infty]} \leq 0.638$, $P > 0.5$ for all cases). Despite this fact, montane summering species were significantly more abundant than both interior and basin summering species ($T_s = 0$, $n = 10$, $P < 0.01$ for both cases). The breeding ranges of montane species, however, tend to extend much farther north and west (typically into western Canada or southern Alaska) than do those of interior and basin species (which often do not extend north to Canada), so that montane species tend to need less misdirection to reach the Farallones than do interior or basin species. Finally, interior summering species, which tend to have more westerly breeding ranges and thus tend to require less misdirection to reach the Farallones than basin summering species, were significantly more abundant than basin summering species ($T_s = 0$, $n = 10$, $P < 0.01$). It appears, therefore, that the fall Farallon abundances of the four summering subgroups relate inversely to the amount of misdirection needed to reach the island.

Vagrant species, while accounting for only 4.0% of the total fall migrants on the Farallones, still occurred in surprisingly large numbers: 1,550 fall individuals in 10 yr. Such a relatively great abundance of vagrants on an offshore California island would have seemed unbelievable only two decades ago. Since then, however, California's birders have discovered that vagrants occur regularly along the entire coast, as well as throughout the desert oases (DeBenedictis 1971, DeSante 1973).

Northern species were the most numerous of the vagrant species and were significantly more abundant than the other three vagrant subgroups ($T_s = 0$, $n = 10$, $P < 0.01$ for all cases). Many northern species have breeding ranges that extend west across Canada to (or sometimes even beyond) the eastern base of the

Rocky Mountains. These species thus require substantially less misdirection to reach the Farallones than do species of the other three vagrant subgroups. In addition, the mean commonness index of northern species was significantly greater than the mean commonness index of southwestern species (Mann-Whitney U -test: $t_{q[\infty]} = 2.114$, $P < 0.05$) but was not significantly different from the mean commonness indices of either southeastern or paleartic species ($t_{q[\infty]} \leq 0.785$, $P > 0.4$ for both cases). No significant differences existed among the mean commonness indices of the other three subgroups ($t_{q[\infty]} \leq 1.950$, $P > 0.05$ for all cases). Southeastern species tended to be more abundant on the Farallones than were southwestern species, which, in turn, tended to be more abundant than paleartic species. The only significant difference, however, was between southeastern and paleartic species ($T_s = -3.0$, $n = 10$, $P < 0.01$). Substantial amounts of misdirection are required for any of these species to reach the Farallones, although it would appear that southeastern species would require less misdirection than either southwestern or paleartic species (minimum misdirections are about 70° for southeastern species, 100° for southwestern species, and 120° for paleartic species). Thus, as in wintering and summering species, the fall Farallon abundance of the four vagrant subgroups appears to relate inversely to the amount of misdirection needed to reach the islands.

Abundance in spring.—Significantly fewer total individual landbirds occurred on the Farallones in spring than in fall (Table 8). This same result also held for the total number of individuals of wintering species and vagrant species (but not for the total number of individuals of summering species) and for seven of the subgroups (coastal, interior, and basin wintering, interior and montane summering, and northern and southwestern vagrants). In contrast, more individuals of coastal summering species and southeastern vagrant species occurred in spring than in fall, but the differences were not significant. Thus, the patterns of differences between fall and spring in number of individuals very nearly matched those same patterns of differences in number of species (Table 3).

In general, the species (or subgroups) that were most abundant in fall were also most abundant in spring. In fact, the total spring

TABLE 8. Differences between fall and spring in the number of *individuals* that occurred on the Farallones as determined by Mann-Whitney *U*-tests.^a

Species group ^b	Mean number of individuals/year		$U_{410,10}$ ^c	P^d
	Fall	Spring		
Wintering				
Coastal	2,976.6 (1,465.2)	452.6 (346.4)	96 (100)	<0.002 (<0.001)
Interior	26.8	2.0	100	<0.001
Montane	1.4 (1.2)	0.4 (0.4)	59 (59)	>0.2 (>0.2)
Basin	8.2	1.4	87	<0.01
Total	3,013.0 (1,501.4)	456.4 (350.2)	96 (100)	<0.002 (<0.001)
Summering				
Coastal	453.1 (445.5)	495.3 (392.9)	61 (64)	>0.2 (>0.2)
Interior	79.6 (79.6)	25.7 (24.1)	97 (97)	<0.002 (<0.002)
Montane	178.0 (167.8)	67.1 (55.1)	95 (99)	<0.002 (<0.001)
Basin	8.3 (8.1)	7.7 (7.5)	51 (50)	>0.2 (>0.2)
Total	719.0 (701.0)	595.8 (479.6)	70 (79)	>0.1 (<0.05)
Vagrant				
Northern	147.6	54.4	90	<0.002
Southeastern	5.5	7.7	64	>0.2
Southwestern	1.7	0.5	80	<0.05
Paleartic	0.2	0.1	55	>0.2
Total	155.0	62.7	90	<0.002
Grand total	3,887.0 (2,357.4)	1,114.9 (892.5)	90 (100)	<0.002 (<0.001)

^a Numbers in parentheses are after the removal of wave days (see text).

^b Classified according to their seasonal and geographical distribution in mainland California (see text).

^c Mann-Whitney *U* statistic.

^d Probability for two-tailed test.

abundance of the 12 subgroups was highly correlated with their total fall abundance (Spearman rank correlation: $r_s = 0.874$, $df = 10$, $P < 0.001$). Within subgroups, the total numbers of individuals of the various species that occurred in spring were also generally well correlated with the total numbers of individuals that occurred in fall, at least for those subgroups that contained over 10 species (Table 9). Inverse correlations between fall and spring, however, did occur for southeastern, southwestern, and palearctic vagrants, but those correlations were not significant.

Individuals of summering species predominated in spring, in marked contrast to fall, and accounted for 53.4% of all spring migrants (Table 6). Their abundance, however, in terms of individuals/species, was not significantly

greater than that of wintering species, which accounted for 40.9% of all spring migrants (Wilcoxon's matched-pairs signed-ranks test: $T_s = 12.0$, $n = 10$, $P > 0.1$). Vagrant species, however, as in fall, were significantly less abundant than both wintering and summering species ($T_s = 0$, $n = 10$, $P < 0.01$ for both cases).

In spring, as in fall, the vast majority of the individuals of wintering species were of the coastal subgroup. They were significantly more abundant than all other subgroups of wintering species ($T_s = 0$, $n = 10$, $P < 0.01$ for all three cases). Apparently, substantial numbers of coastal wintering species migrate north, back up the coast in spring, and can occur on the Farallones with little or no misdirection. The remaining three subgroups of wintering species were all very scarce; combined, they accounted

TABLE 9. Spearman rank correlations (r_s) between the total number of individuals of each species that occurred on the Farallones in fall and spring.^a

Species group ^b	Total number of species	r_s	P^c
Wintering			
Coastal	54	0.858 (0.855)	<0.001 (<0.001)
Interior	9	0.417	—
Montane	5	0.850 (0.600)	— (—)
Basin	4	0.800	—
Summering			
Coastal	27	0.696 (0.673)	<0.001 (<0.001)
Interior	22	0.729 (0.722)	<0.001 (<0.001)
Montane	16	0.565 (0.536)	<0.05 (<0.05)
Basin	6	0.257 (0.257)	— (—)
Vagrant			
Northern	42	0.697	<0.001
Southeastern	20	-0.164	>0.1
Southwestern	9	-0.317	—
Palearctic	3	-0.500	—

^a Numbers in parentheses are after the removal of wave days (see text).

^b Classified according to their seasonal and geographical distribution in mainland California (see text).

^c Probabilities are given only when sample size (total number of species) is greater than 10. Degrees of freedom = total number of species - 2.

for less than 0.4% of the total spring individuals. Basin species were slightly more abundant than interior species, although the difference was not significant ($T_s = 13.5$, $n = 10$, $P > 0.1$). Montane species, as in fall, were extremely scarce, were significantly less abundant than basin species ($T_s = 6.0$, $n = 10$, $P < 0.05$), and tended to be less abundant than interior species ($T_s = 2.5$, $n = 7$, $P < 0.05$ one-tailed).

In spring, as in fall, coastal species were the most numerous of the summering species and were significantly more abundant than the other three subgroups ($T_s = 0$, $n = 10$, $P < 0.01$ for all cases). Coastal summering species were, in fact, the most abundant species on the Farallones in spring and were even significantly more abundant than coastal wintering species ($T_s = 6.0$, $n = 10$, $P < 0.05$). This is not unexpected, because substantial numbers of individuals of coastal summering species are mi-

TABLE 10. Frequency distributions of the number of individuals that arrived on the Farallones each day during September and October (Fall) and April and May (Spring) during the 10 yr of study.

Number of arriving individuals	Frequency (number of days)	
	Fall (Sept and Oct)	Spring (Apr and May)
0	21	138
1-5	179	283
6-10	92	75
11-25	121	52
26-50	80	28
51-100	64	19
101-150	24	4
151-200	8	1
201-250	8	5
251-300	3	1
301-350	2	0
351-400	1	0
401-500	1	1
501-600	1	1
601-800	0	2
801-1,000	0	0
1,001-2,000	3	0
>2,000	2	0
Total	610	610

} Wave days

grating in spring toward their coastal breeding grounds, thus nearly directly toward the Farallones, and, like coastal wintering species in fall, could reach the islands with little or no misdirection. Montane species were the next most numerous subgroup of summering species and, as in fall, were significantly more abundant than both interior and basin summering species ($T_s = 0$, $n = 10$, $P < 0.01$ for both cases). In contrast to fall, basin summering species slightly outnumbered interior summering species, but the difference was not significant ($T_s = 18.5$, $n = 9$, $P > 0.2$).

Vagrant species accounted for 5.6% of the total spring individuals, a small but substantial portion. Spring abundances of the four vagrant subgroups rather closely paralleled their fall abundances, with northern species being the most common, followed, in turn, by southeastern, southwestern, and finally palearctic species. All of the differences were significant ($T_s \leq 1.5$, $n = 10$, $P < 0.01$ for all five cases) except the difference between southwestern and palearctic species ($T_s = 6.0$, $n = 6$, $P > 0.2$). It thus appears that the Farallon abundance of the various subgroups in spring, as well as in fall,

generally relates inversely to the amount of misdirection needed to reach the islands.

ANNUAL VARIATION IN ABUNDANCE

Table 4 indicates that a substantial amount of year-to-year variation existed, in both fall and spring, in the number of individuals in each subgroup that occurred on the Farallones. The hypothesis that the mean number of total individuals (3,887.0 in fall, 1,114.9 in spring) was invariant over the 10 yr was rejected for both seasons ($\chi^2 = 29,303.4$, $df = 9$, $P \ll 0.001$ in fall, $\chi^2 = 2,825.8$, $df = 9$, $P \ll 0.001$ in spring). This same result also held true for the total wintering, summering, and vagrant groups in both fall and spring ($\chi^2 \geq 247.9$, $df = 9$, $P \ll 0.001$ for all cases) and for all nine subgroups in fall and seven subgroups in spring for which the mean (expected) number of individuals was greater than 5.0 ($\chi^2 \geq 39.2$, $df = 9$, $P < 0.001$ for all 16 cases except southeastern vagrants in fall and spring for which $\chi^2 = 19.0$, $df = 9$, $P < 0.05$ and $\chi^2 = 22.4$, $df = 9$, $P < 0.01$, respectively). Highly significant year-to-year variations thus occurred in the number of *individuals* that reached the Farallones, despite the fact that the number of *species* remained statistically invariant.

Not only did the number of individuals vary significantly from year to year, the relative proportions of wintering, summering, and vagrant individuals also varied significantly over the 10 yr in both fall ($\chi^2 = 5,139.0$, $df = 18$, $P \ll 0.001$) and spring ($\chi^2 = 1,556.3$, $df = 18$, $P \ll 0.001$). Thus, certain falls (1972, 1968, 1970) were best for individuals of wintering species, while other falls (1974, 1972, 1975) were best for individuals of summering and vagrant species. Similarly, the best springs for individuals of wintering species (1973, 1971, 1969) were somewhat different from the best springs for individuals of summering (1969, 1971, 1970) or vagrant species (1975, 1977, 1969).

Furthermore, the relative proportions of the four subgroups of summering individuals also varied significantly over the 10 yr in both fall ($\chi^2 = 172.3$, $df = 27$, $P \ll 0.001$) and spring ($\chi^2 = 199.7$, $df = 27$, $P \ll 0.001$), as did the three subgroups of wintering individuals in fall (coastal, interior, and basin) that had a mean (expected) number of individuals greater than 5.0 ($\chi^2 = 401.5$, $df = 18$, $P \ll 0.001$). In contrast, however, the relative proportions of northern

and southeastern vagrant individuals (the only vagrant subgroups that had mean abundances greater than 5.0) remained invariant over the 10 yr in both fall ($\chi^2 = 4.5$, $df = 9$, $P > 0.5$) and spring ($\chi^2 = 9.5$, $df = 9$, $P > 0.1$).

WAVE DAYS

The frequency distributions of the number of individuals that arrived each day during fall (September and October only) and spring (April and May only) over the entire 10 yr of study are presented in Table 10. These distributions were much as might be expected for daily migration data: large numbers of days when few birds (or, in spring, none) arrived and few days when large numbers arrived. Of particular interest are those very few days when truly exceptional numbers of birds arrived. There were five such days in fall (29 Sept. 1968, 11 Oct. 1969, 7 Oct. 1970, and 2 and 3 Oct. 1972, when 2,694, 1,197, 1,189, 9,144, and 1,317 individuals, respectively, arrived) and four such days in spring (8 May 1969, 30 April and 9 May 1971, and 4 April 1973, when 721, 547, 422, and 632 individuals, respectively, arrived). I refer to these days as wave days.

It is of considerable interest that the total number of individuals of wintering and summering groups was greatly increased on wave days but that the total number of vagrant individuals was not. This was determined by comparing (by means of Mann-Whitney *U*-tests) the number of individuals of each subgroup that occurred on the 5 fall wave days (or 4 spring wave days) with the number that occurred on the other 45 fall days (or 36 spring days) of the same dates during the 10 yr (Table 11). Five subgroups were significantly affected by wave days during fall (coastal and montane wintering, and coastal, montane, and basin summering) and five were significantly affected in spring (coastal wintering, and coastal, interior, montane, and basin summering). Vagrant subgroups were not significantly affected in either fall or spring. This result might be expected in spring, because most vagrants occur in very late May or June, well after the time of spring wave days (DeSante and Ainley 1980). It was an unexpected result in fall, however, because large numbers of vagrants do occur during late September and early October, at just the time of fall wave days (DeSante and Ainley 1980).

TABLE 11. Differences between the number of individuals that occurred on the Farallones on wave days and nonwave days as determined by Mann-Whitney *U*-tests.

Species group ^a	Fall					Spring				
	Mean number		<i>U</i> _[45,5] ^d	<i>t</i> _[∞] ^e	<i>P</i> ^f	Mean number		<i>U</i> _[36,4] ^d	<i>t</i> _[∞] ^e	<i>P</i> ^f
	Wave days ^b	Non-wave days ^c				Wave days ^g	Non-wave days ^h			
Wintering										
Coastal	3,058.6	38.9	225.0	3.64	<0.001	271.3	7.6	143.0	3.36	<0.001
Interior	0.6	0.6	112.5	0.00	>0.9	0.3	0.1	85.5	1.37	>0.1
Montane	0.4	0.0	157.5	4.29	<0.001	0.0	0.0	—	—	—
Basin	0.2	0.2	116.5	0.20	>0.5	0.0	0.0	—	—	—
Total	3,059.8	39.7	225.0	3.64	<0.001	271.5	7.6	143.0	3.36	<0.001
Summering										
Coastal	17.8	3.7	201.5	2.92	<0.01	263.3	8.5	138.0	3.13	<0.005
Interior	0.2	0.4	119.5	0.30	>0.5	4.0	0.3	139.0	4.24	<0.001
Montane	20.8	1.4	201.0	3.05	<0.01	31.0	1.4	141.0	3.83	<0.001
Basin	0.4	0.1	150.0	2.33	<0.02	0.5	0.1	103.0	2.75	<0.01
Total	39.2	5.6	203.5	2.96	<0.01	298.7	10.3	140.0	3.13	<0.005
Vagrant										
Northern	2.4	2.6	124.0	0.38	>0.5	0.3	0.1	83.0	0.98	>0.2
Southeastern	0.4	0.0	133.0	1.95	<0.1	0.0	0.0	—	—	—
Southwestern	0.0	0.0	—	—	—	0.0	0.0	—	—	—
Palaearctic	0.0	0.0	—	—	—	0.0	0.0	—	—	—
Total	2.8	2.6	136.0	0.78	>0.4	0.3	0.1	83.0	0.98	>0.2
Grand total	3,101.8	47.9	225.0	3.64	<0.001	570.5	18.1	144.0	3.27	<0.005

^a Classified according to their seasonal and geographical distribution in mainland California (see text).

^b 29 September 1968, 11 October 1969, 7 October 1970, and 2 and 3 October 1972.

^c All other 29 September and 2, 3, 7, and 11 October dates for the 10-yr period.

^d Mann-Whitney *U* statistic for [*n*₁, *n*₂].

^e Statistic used when *n* > 20. Compared to Student's *t*-distribution for *df* = ∞.

^f Probability for two-tailed test.

^g 8 May 1969, 30 April and 9 May 1971, and 4 April 1973.

^h All other 4 and 30 April and 8 and 9 May dates for the 10-yr period.

Because such a substantial proportion of the individuals that occurred on the Farallones arrived on the few wave days (40.0% of all fall individuals and 20.8% of all spring individuals), it was deemed advisable to re-analyze completely all of the data after excluding wave days. One cannot, however, simply throw out all the data from wave days, because wave days tend to occur during the peak of fall and spring migration, and a substantial number of birds "should" have arrived then anyway. To overcome this difficulty, I replaced, for each species in each of the subgroups that was found to be significantly affected by wave days, the number that arrived on the wave day with the mean number that arrived on that date in the other 9 yr. The adjusted numbers that resulted from this "removal" of wave days are shown in Table 4 and in subsequent tables in parentheses.

It is most interesting to note that this adjustment for wave days had absolutely no effect

on any of the relative abundances of any of the subgroups in either fall or spring or on any of the significance values resulting from statistical tests that either compared the abundances of subgroups or determined the correlations of abundance and commonness except for one case: the significance of the difference between fall and spring in the total number of individuals of summering species (fall > spring) was increased from *P* > 0.1 to *P* < 0.05 after the removal of wave days.

It is also important to note that the "removal" of wave days had no effect on the significance of the amount of annual variation for any of the groups or subgroups in either fall or spring or upon the significance of the amount of annual variation in the relative proportions of the various groups or subgroups in either fall or spring. The χ^2 values were, of course, reduced, but all affected significance values remained *P* < 0.001. Thus, the highly significant

amounts of year-to-year variation in the number of individuals of the various subgroups and in the relative proportions of individuals in the various subgroups did not simply result from the occurrences of a few massive landbird waves on the Farallones but were intrinsic to the entire Farallon data base.

DISCUSSION

CAUSES OF THE FARALLON OCCURRENCES OF LANDBIRDS

A large majority of the individual landbirds that arrived on Southeast Farallon during fall migration were young of the year. In fact, 82.8% of 3,503 individuals aged by skull pneumatization during the falls of 1968-1972 were immatures. A high proportion of immatures, however, is characteristic of populations of migrant landbirds on both the west coast (Ralph 1971, Stewart et al. 1974) and the east coast (Ralph 1981). It has been suggested that the coasts are the edges of the migratory routes of many species and that many of the immatures found along the coast (or on offshore islands) during fall migration are off-course and probably perish (Ralph 1981).

While immatures can be aged accurately during fall by their incomplete skull pneumatization, no general method of aging most species of live birds in spring has yet proven reliable. PRBO is presently investigating the wing-wear characteristics of known-age birds at the Palomarin Field Station in order to test the hypothesis that spring individuals with excessively worn wings tend to be second-year birds. If this hypothesis proves correct, then many spring migrants on the Farallones may be assumed to be second-year birds on their first spring migration, as many of them have very worn wings. It would not be surprising if substantial numbers of spring migrants on the Farallones were second-year birds that lacked some navigational capacity and that probably perish. In fact, the recovery rate of Farallon-banded birds was significantly lower than that of birds banded at Palomarin, 33 km northeast on the immediate mainland coast (DeSante and Ainley 1980). A detailed analysis of the age structure of Farallon migrant landbirds will be the subject of a future paper.

Although the landbird species that occurred on Southeast Farallon originated from

throughout North America, the great majority of the individuals (88.3% in fall and 85.0% in spring) were of species that either winter or breed along the central California coast and that would be expected to migrate in substantial numbers either along or relatively near to the coast. It is not surprising, therefore, that individuals of coastal species predominated on those occasions, in either fall or spring, when massive waves of landbirds inundated the Farallones. Coastal wintering species were more strongly affected by these waves in fall, when they tend to be migrating toward the Farallones, than in spring, when they tend to be migrating away from the coast toward breeding areas variously located throughout western North America. In fact, 50.8% of the fall coastal wintering individuals arrived on the 5 fall wave days but only 23.5% of the spring coastal wintering individuals arrived on the 4 spring wave days. Similarly, coastal summering species were more strongly affected by these waves in spring, again when they tend to be migrating toward the island, than in fall, when they tend to be migrating away from the coast toward wintering grounds in Mexico and Central America. Thus, 20.7% of the spring coastal summering individuals arrived on the 4 spring wave days, but only 1.7% of the fall coastal summering individuals arrived on the 5 fall wave days.

It seems likely that these massive waves of landbirds could have resulted from relatively minor changes in local weather conditions, which caused large numbers of normal on-course migrants to drift slightly offshore or to overshoot the coast. It also seems likely that substantial numbers of adults, which were returning to coastal wintering or breeding areas, could have been included in these waves. The fact that the percentage of immatures in a number of coastal wintering species was significantly lower on fall wave days than on fall nonwave days (Stewart et al. 1974) lends support to this suggestion. The local weather factors associated with these waves are presently under investigation but appear to involve some combination of low pressure, precipitation, electromagnetic disturbance, and offshore winds.

The remaining noncoastal species whose normal migration routes pass through California (interior, montane, and basin species) were also generally affected by wave days in both fall and spring, but the magnitude of the effect

was much less. Furthermore, the magnitude of the wave effect appeared to be directly related to the abundance of the subgroups on the Farallones and thus inversely related to the amount of misdirection needed to reach the islands, as Farallon abundance itself was inversely related to the amount of misdirection needed to reach the islands. Thus, the percentages of all spring occurrences of the summering subgroups that occurred on the four spring wave days were: coastal 20.7%, montane 17.9%, interior 6.2%, and basin 2.6%. It appears, therefore, that these interior, montane, and basin species can be affected by local weather when they are on the coast but that their occurrences on the coast are governed by factors other than local weather.

Vagrants, which need the greatest degree of misdirection to reach the Farallones, were not affected by wave days at all. This is reasonable, because these individuals, by virtue of their breeding ranges alone, must have followed flight paths toward the Farallones that ultimately led to an offshore flight. Local weather could have delayed or displaced them north or south but would not necessarily have altered the numbers occurring on the island, because approximately equal numbers should reach the coast both to the north and south.

It is likely that a number of different mechanisms can cause vagrancy in migratory birds. These mechanisms probably differ between immatures in fall, which apparently use simple compass orientation to reach their wintering grounds, and second-year birds in spring or adults at any season, which presumably use some degree of true bi-coordinate navigation. Because we have relatively incomplete knowledge of how adult birds determine map coordinates or their current location, it is not surprising that relatively few mechanisms have been proposed to explain navigational errors.

Several mechanisms for explaining orientational errors, however, can be suggested. These include disorientation (the inability of an individual bird to follow any consistent orientation) and misorientation (the inability of an oriented bird to follow the correct orientation). Disorientation could arise from a failure to inherit any compass direction or from a failure to learn a consistent compass reference point. Three mechanisms for misorientation can be described. The first, simple compass misorientation, involves a bird simply inheriting a wrong compass direction or learning a wrong

compass reference point. Theoretically, all angles of misorientation are possible, although natural selection may cause larger angles of misorientation to be less frequent than smaller ones. The second mechanism, 180° reverse misorientation, involves a bird following a northward direction in fall that would be appropriate for its return to the breeding grounds in spring. The third mechanism, mirror-image misorientation, involves the confusion or non-discrimination of right and left in relating an inherited migration direction to a compass reference point. Such a bird would orient along the mirror-image (with respect to the axis containing the compass reference point, the north-south axis) of the correct direction (west instead of east, southwest instead of southeast).

It seems likely that all mechanisms of disorientation and misorientation have been responsible, to some degree or another, for the occurrences of vagrant landbirds on the Farallones. Analyses of the timing, relative abundances, and relative locations of occurrences of the various species of vagrant wood warblers in California, however, along with orientation cage results on Farallon-captured fall vagrant Blackpoll Warblers (*Dendroica striata*), led me to suggest that mirror-image misorientation may be an important, if not predominate, mechanism causing the occurrences of vagrant landbirds in California and on the Farallones (DeSante 1973).

Clearly, a large number of very diverse factors must be operative to cause the widely varying abundances of the many landbird species that occur on the Farallones. Some of these factors might be as follows. (1) The total number of individuals in the source population. DeBenedictis (1971) showed that the size of the source population accounted for nearly 60% of the variation in abundance of vagrant wood warblers and vireos in California. In contrast, this study shows that source population size only accounted for about 30% of the variation in Farallon abundance of the various species in any subgroup or for the variation in mean Farallon abundance of the various subgroups themselves. (2) The population density in that part of each species' range nearest the Farallones. A difficulty with the first correlation is that a species that has a relatively small total source population, but that is very common on the mainland near the Farallones, may be inordinately abundant on the island. A good example is the Golden-crowned Sparrow

(*Zonotrichia atricapilla*), which, with the exception of the Starling, is the most abundant fall landbird on the Farallones. The reverse situation can also occur. A species with a fairly large total source population may be very rare in that part of its range nearest the Farallones and thus be less abundant on the Farallones than expected from source-population size alone. The Yellow-billed Cuckoo (*Coccyzus americanus*) is a good example. (3) The propensity of a species to migrate and the regularity of its migrations. DeSante and Ainley (1980) showed that non-migratory species or nonmigratory populations of migratory species simply do not occur on the Farallones. (4) Whether the species migrates nocturnally or diurnally. Diurnal migrants are generally much less common on the Farallones than are nocturnal migrants (DeSante and Ainley 1980). (5) The evolutionary history of the species' migratory behavior. DeSante and Ainley (1980) showed that 10-primaried passerines were significantly less abundant on the Farallones in fall than were 9 primaried passerines. (6) The location of the species' breeding and winter ranges relative to the Farallones, that is, the angle of misorientation needed to reach the island. Both this study and DeBenedictis (1971) provided evidence that species (or groups of species) become less abundant on the Farallones (or in California) as the angle of misorientation needed to reach the island increases. My earlier work (DeSante 1973) suggests that this perhaps should be modified to include the angle of misorientation from the mirror-image of the correct direction as well. Other factors potentially influencing Farallon abundance might include the seral stage in which the species breeds (or winters) and the species' rate of population turnover (DeBenedictis 1971). Further discussion of these factors, however, is beyond the scope of this paper. A multivariate analysis of these factors will be the subject of a future paper.

CAUSES OF ANNUAL VARIABILITY

The coefficient of variation (CV) of the total number of individuals over the 10 yr was presented for each subgroup in Table 4A (fall) and 4B (spring). These CV's are plotted as a function of the natural logarithm of the total number of individuals for 11 of the 12 subgroups in both fall and spring in Fig. 2A (before) and 2B (after) the "removal" of wave days. Palearc-

tic vagrants were excluded, because their very low numbers (only 2 individuals in 10 falls and 1 individual in 10 springs) necessarily produced extremely high CV's. A logarithmic scale was used, because the total numbers of individuals varied by a factor of over 2,000, while the CV's varied only by a factor of about 6.

As expected from statistical considerations alone, high variability was generally associated with low total numbers of individuals. There were some noteworthy exceptions, however, in that coastal wintering species in fall and coastal summering and coastal wintering species in spring, which had the highest total numbers of individuals of any of the subgroups in those seasons, had relatively high CV's (Fig. 2A). The relatively high variability of these groups was caused by the large numbers of individuals that occurred on the few fall and spring wave days. When these wave days were "removed," their CV's dropped dramatically (Fig. 2B).

Montane wintering species, despite their very low total numbers in both fall and spring, appeared to have relatively high variability in both seasons, even after the removal of wave days (Figs. 2A and 2B). High annual variability, however, is characteristic of the mainland invasions of these highly sporadic winter irruptive species, which in many falls do not migrate at all. High annual variability on the Farallones, therefore, is not surprising. Finally, it is interesting to note that when these irruptive montane wintering species were removed (and when wave days were removed), the relationship between variability and total abundance for the remaining 10 subgroups was nearly identical in fall and spring in terms of both y -intercept (107.0 in fall, 109.4 in spring) and slope (-8.6 in fall, -8.5 in spring). This implies that the remaining factors causing annual variability in the number of landbirds arriving on the Farallones operate in a consistent manner on all species in both fall and spring.

What might these factors be? Three possibilities at once come to mind: (1) local weather conditions acting near the Farallones (in addition to those conditions presumably causing wave days); (2) large-scale, long-range weather conditions acting over large areas of the continent; and (3) the number of young produced each summer and their subsequent winter survival.

Local weather certainly can affect the number of landbirds arriving on the Farallones.

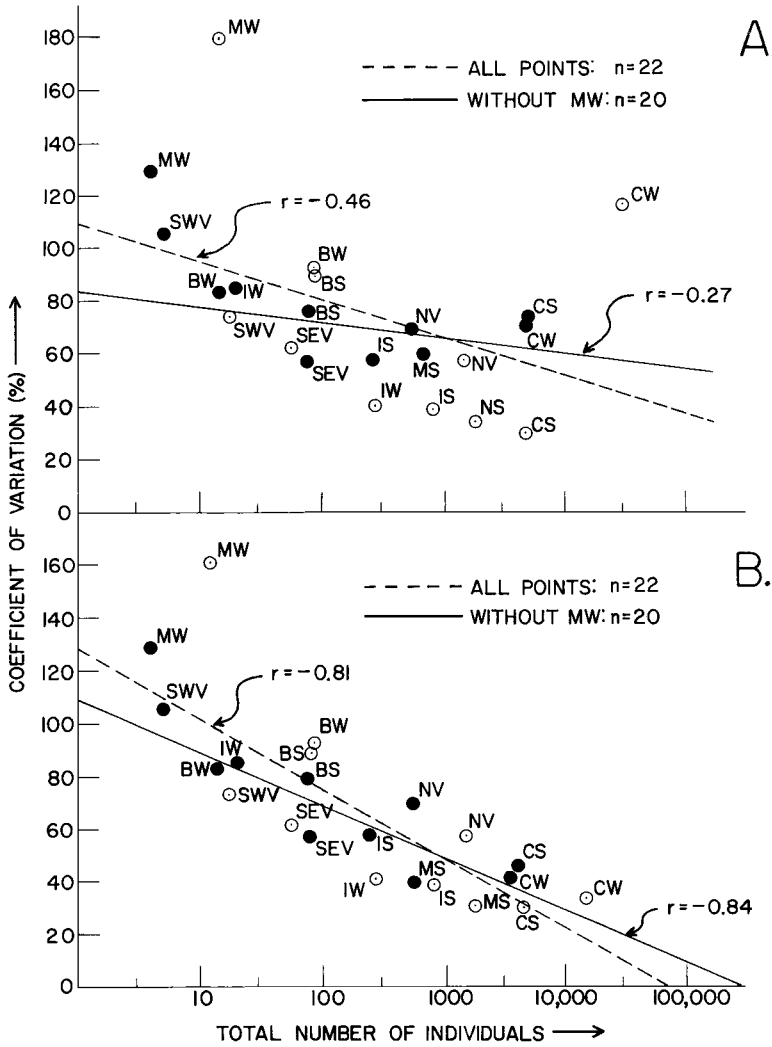


Fig. 2. The fall (○) and spring (●) year-to-year variability (over 10 yr, fall 1968–spring 1978) of migrant landbirds on Southeast Farallon Island as a function of abundance before (A) and after (B) the removal of wave days. CW, IW, MW, BW = coastal, interior, montane, and basin wintering subgroups; CS, IS, MS, BS = coastal, interior, montane, and basin summering subgroups; NV, SEV, SWV = northern, southeastern, and southwestern vagrant subgroups.

Many arrive after dawn and most appear to be returning toward the mainland when they find the island. Thus, visibility must play a key role. In fact, it appears that the number of landbirds arriving on the island is generally low, both when the island is shrouded in fog and when the mainland is clearly visible from a great distance (DeSante and Ainley 1980). The number of arrivals is also low when winds are strong out of the west or northwest. Apparently, few birds get out over the ocean on such occasions.

Local weather, however, cannot account for all of the observed annual variations in numbers. This is supported by two lines of evidence. First, the proportions of the four subgroups of summering species, which all tend to arrive on the island at roughly the same time (DeSante and Ainley 1980) and thus would be expected to be influenced in the same manner by the same local weather factors, varied significantly from year to year in both fall and spring. Similarly, the proportions of three win-

TABLE 12. Maximum range of annual variation (after the removal of wave days, see text) in the number of individuals arriving on the Farallones.

Species group ^a	Number of individuals arriving in a given year					
	Fall			Spring		
	Max.	Min.	Ratio (max/min)	Max.	Min.	Ratio (max/min)
Wintering						
Coastal	2,309	827	2.79	620	125	4.96
Interior	42	14	3.00	5	0	—
Montane	6	0	—	1	0	—
Basin	26	0	—	3	0	—
Total	2,335	859	2.72	622	127	4.90
Summering						
Coastal	636	215	2.96	774	211	3.67
Interior	130	37	3.51	45	8	5.65
Montane	283	86	3.29	107	35	3.06
Basin	27	3	9.00	21	0	—
Total	1,055	387	2.73	926	260	3.56
Vagrant						
Northern	342	68	5.03	141	12	11.75
Southeastern	11	2	5.50	18	2	9.00
Southwestern	4	0	—	1	0	—
Palaearctic	1	0	—	1	0	—
Total	354	72	4.92	160	15	10.67
Grand total	3,333	1,642	2.02	1,447	530	2.73

^a Classified according to their seasonal and geographical distribution in mainland California (see text).

tering subgroups, which also tend to arrive at roughly the same time in fall although later than summering species (DeSante and Ainley 1980), also varied significantly from fall to fall. Second, the number of vagrants (at least of wood warblers) that were recorded in California as a whole also varied greatly from year to year, and these variations tended to correlate fairly well with variations on the Farallones (DeSante 1973, Shuford 1981). Thus, factors in addition to local weather must be operative to cause the annual variations in the proportions of the various summering and wintering subgroups on the Farallones and to cause the annual variations in the numbers of vagrants that occur in California as a whole.

Because most fall Farallon individuals were immatures, it might be expected that the annual variation in the numbers of Farallon individuals could reflect, at least in fall, fluctuations in the production of young during the preceding summer. Unfortunately, measurements of annual productivity of given landbird species or groups of species generally do not exist except for very small study areas where either nests or the number of dispersing juve-

niles can be monitored. The Point Reyes Bird Observatory has been monitoring the number of dispersing juveniles (primarily of coastal summering species) at its Palomarin Field Station for the past 8 yr and has found that annual productivity has varied, between drought and heavy rainfall years, by a factor of about three (DeSante MS). Interestingly, the number of fall Farallon individuals (after removing wave days) of wintering and summering groups also showed a roughly threefold variation over the 10 yr (Table 12). If variations in productivity similar to that found at Palomarin could exist synchronously over extensive areas of the breeding ranges of a number of these species, then these variations could well be a major cause of the variations in fall abundance on the Farallones, at least for these western species. Table 12 indicates, however, that the variation in the number of fall Farallon individuals of vagrant species was somewhat greater than that of western species—about fivefold. This would imply either that these vagrant species have greater annual variations in productivity than western species or that still other factors must contribute to the variability of fall vagrant oc-

TABLE 13. Spearman rank correlations (r_s) between the total number of individuals that arrived on the Farallones in a given fall and the number that arrived the following spring, and between the number that arrived in a given spring and the number that arrived the following fall.^a

Species group ^b	Fall to following spring (sample size = 10)			Spring to following fall (sample size = 9)		
	r_s	$(r_s)^2$	P^c	r_s	$(r_s)^2$	P^c
Wintering						
Coastal	0.491 (0.361)	0.241 (0.130)	>0.1 (>0.1)	-0.450 (-0.404)	0.203 (0.163)	>0.1 (>0.1)
Interior	0.552	0.305	<0.1	0.246	0.061	>0.1
Montane	0.633	0.401	<0.05	0.063	0.004	>0.1
Basin	-0.027	0.001	>0.1	-0.150	0.023	>0.1
Total	0.491 (0.382)	0.241 (0.146)	>0.1 (>0.1)	-0.450 (-0.433)	0.203 (0.187)	>0.1 (>0.1)
Summering						
Coastal	-0.248 (-0.273)	0.062 (0.075)	>0.1 (>0.1)	-0.017 (0.033)	0.000 (0.001)	>0.1 (>0.1)
Interior	0.173 (0.094)	0.030 (0.009)	>0.1 (>0.1)	-0.233 (-0.054)	0.054 (0.003)	>0.1 (>0.1)
Montane	0.030 (0.164)	0.001 (0.027)	>0.1 (>0.1)	-0.383 (-0.217)	0.147 (0.047)	>0.1 (>0.1)
Basin	0.448	0.201	>0.1	-0.533	0.284	>0.1
Total	-0.188 (-0.285)	0.035 (0.081)	>0.1 (>0.1)	-0.133 (-0.067)	0.018 (0.004)	>0.1 (>0.1)
Vagrant						
Northern	0.285	0.081	>0.1	0.450	0.203	>0.1
Southeastern	0.342	0.117	>0.1	0.250	0.063	>0.1
Southwestern	-0.309	0.095	>0.1	0.425	0.181	>0.1
Palaearctic	0.561	0.315	<0.1	0.663	0.440	<0.1
Total	0.224	0.050	>0.1	0.450	0.203	>0.1
Grand total	0.782 (0.358)	0.612 (0.128)	<0.01 (>0.1)	-0.267 (-0.417)	0.071 (0.174)	>0.1 (>0.1)
Mean		0.154 (0.146)			0.139 (0.119)	

^a Numbers in parentheses are after the removal of wave days (see text).
^b Classified according to their seasonal and geographical distribution in mainland California (see text).
^c Degrees of freedom = sample size - 2.

currences on the Farallones. Table 12 also indicates that greater maximum annual variations tend to occur in spring than in fall.

If annual variations in the production of young were primarily responsible for annual variations in the occurrences of landbirds on the Farallones, then we might expect that the number of individuals on the island in any given spring should be positively correlated with the number present the previous fall. In other words, if large numbers of young are produced in a given year, many birds will be available to make orientation errors in their first fall migration, and many successful fall migrants will be available to make some navigation errors in their first spring migration. Table 13 presents, for each subgroup, the results of Spearman rank

correlations on these data. Although 9 of the 12 subgroups displayed positive correlations between the number of individuals in fall and the number the following spring, in only one subgroup, montane wintering species, was the correlation significant ($P < 0.05$). Furthermore, the mean r_s^2 value for the various subgroups for the correlation between a given fall and the following spring was not significantly different from the mean r_s^2 value for the correlation between a given spring and the following fall (Mann-Whitney U -tests: $U_{[12,12]} = 79$ including wave days, $U_{[12,12]} = 59.5$ excluding wave days, $P > 0.2$ for both cases). Table 13 also indicates that only 6 of the 12 spring-to-fall correlations were positive and that none of them was significant. This indicates that the significant (P

< 0.01) fall-to-spring correlation that was found for total individuals before the removal of wave days (Table 13) was probably spurious. It also indicates that, if annual variations in productivity are the driving force for annual variations in fall Farallon occurrences, these annual variations in productivity are so strongly (and probably randomly) affected by winter survival that they are not the driving force for annual variations in spring Farallon occurrences.

It is interesting that the only subgroup showing significant correlation between fall and spring numbers was the montane wintering one. Because these highly irruptive species migrate at all in only a few winters, this correlation would be expected without regard to productivity.

It seems likely that long-range, large-scale weather factors may also be important in causing the annual variations in the numbers of landbirds, particularly the number of vagrants, reaching the Farallones. Recall that the relative proportions of northern and southeastern vagrant individuals remained statistically invariant over the 10 yr in both fall and spring. Thus, good years for northern vagrants also tended to be good years for southeastern vagrants. It seems unlikely that productivity would vary synchronously over such large areas of the continent. Large-scale weather systems, however, might. The truly exceptional numbers of eastern vagrants to the Farallones in the fall of 1974 were also documented from mainland California and the entire western United States (Crowell and Nehls 1975, Kingery 1975, McCaskie 1975, Mills et al. 1975, Rogers 1975, Stallcup et al. 1975). Zimmerman (1975) discussed this "spectacular displacement of eastern passerines westward" and agreed with Stallcup et al. (1975) that large-scale weather factors played a key role. The operation of these factors may best be understood through methods of synoptic analysis (e.g. Richardson 1978). The position, timing, duration, intensity, and movement of high- and low-pressure systems and fronts, and the winds they produce, may well be found to be proximally responsible for the annual variations in the Farallon occurrences of vagrant birds.

CHANGES IN ABUNDANCE

Variations in annual productivity and in both long-range and local weather conditions would

be expected to produce random, or perhaps cyclic, variations in the number of landbirds reaching the Farallones. Over a long period of time, unless other factors are operative, the number of migrant landbirds on the Farallones should remain constant. It is important, therefore, to ask whether or not any of the subgroups have shown significant changes in abundance during the 10 yr of the study. Ten years, of course, is not really long-term, but it will serve as a start toward answering this question. The high annual variability of most subgroups precludes a reliable regression analysis, but the number of individuals of each species that occurred during the first 5 yr can be compared to the number that occurred during the second 5 yr by means of a Wilcoxon matched-pairs signed-ranks test. These results are shown in Table 14.

Wintering species decreased in fall ($P < 0.001$), and summering species decreased in spring ($P < 0.05$) during the second 5 yr of this study. These decreases, however, resulted from the lack of wave days during the second 5 yr, because, when wave days were removed, neither of the decreases was significant. Only the decrease in coastal wintering species remained barely significant ($P < 0.05$) after the removal of wave days. Vagrants, on the other hand, significantly increased during the second 5 yr in both fall ($P < 0.001$) and spring ($P < 0.02$). This increase was most pronounced in northern vagrants, which showed highly significant increases ($P < 0.001$) in both fall and spring.

Many authors have noted the greatly increased number of vagrant sightings in recent years, particularly of eastern passerines in the west (Able 1972, Zimmerman 1975, DeSante 1976, Kaufman 1977, Smith 1977, DeBenedictis 1978, Schimpf and Smith 1979, Shuford and DeSante 1979), but also of certain passerines in Nova Scotia (McLaren 1981). Most of these results, however, are plagued with observational biases. Are there more vagrant landbirds, or are there simply more observers with a better knowledge of how, when, and where to find them and who supply more thorough coverage of localities favored by vagrants? The Farallon data are virtually free of observational bias, and the conclusion is straightforward: numbers of vagrants, especially northern vagrants, did increase during the second 5 yr of this study.

Why? Four hypotheses seem worth pursuing in the hope that data may become available to

TABLE 14. Summary of the differences between the first and second 5 yr in the number of migrant landbirds on Southeast Farallon Island as determined by Wilcoxon's matched-pairs signed-ranks test.^a

Species group ^b	Fall					Spring				
	Total number of individuals		T _s ^c	n ^d	P ^e	Total number of individuals		T _s ^c	n ^d	P ^e
	1968-1972	1973-1977				1969-1973	1974-1978			
Wintering										
Coastal	23,588 (8,474)	6,178 (6,178)	199.5 (349.5)	51 (47)	<0.01 (<0.05)	2,931 (1,869)	1,595 (1,595)	267.5 (299.0)	38 (39)	>0.1 (>0.1)
Interior	122	146	13.0	8	>0.1	6	14	1.0	4	—
Montane	9 (7)	5 (5)	3.0 (5.5)	5 (5)	>0.1 (>0.1)	2	2	1.5	2	—
Basin	39	43	4.0	4	—	5	9	0.0	2	—
Total	23,758 (8,642)	6,372 (6,372)	532.5 (766.5)	68 (64)	<0.001 (<0.1)	2,944 (1,882)	1,620 (1,620)	460.0 (394.0)	46 (47)	>0.1 (<0.1)
Summering										
Coastal	2,109 (2,033)	2,422 (2,422)	132.5 (116.0)	24 (23)	>0.1 (>0.1)	3,383 (2,359)	1,570 (1,570)	106.5 (123.0)	25 (25)	>0.1 (>0.1)
Interior	359	437	75.0	18	>0.1	149 (133)	108 (108)	21.5 (24.5)	13 (12)	>0.1 (>0.1)
Montane	907 (805)	873 (873)	44.0 (42.5)	13 (14)	>0.1 (>0.1)	412 (292)	259 (259)	27.5 (53.0)	15 (15)	<0.1 (>0.1)
Basin	37 (35)	46 (46)	8.5 (4.5)	6 (5)	>0.1 (>0.1)	33 (31)	44 (44)	5.0 (4.5)	6 (6)	>0.1 (>0.1)
Total	3,412 (3,332)	3,778 (3,778)	864.5 (767.5)	61 (60)	>0.1 (>0.1)	3,977 (2,815)	1,981 (1,981)	613.5 (720.0)	59 (58)	<0.05 (>0.1)
Vagrant										
Northern	530	946	138.5	42	<0.001	187	357	89.0	30	<0.001
Southeastern	21	34	22.0	12	>0.1	35	42	37.5	12	>0.1
Southwestern	7	10	5.0	5	>0.1	3	2	2.0	3	—
Paleartic	1	1	1.5	2	—	1	0	1.0	1	—
Total	559	991	366.0	61	<0.001	226	401	317.0	46	<0.02

^a Numbers in parentheses are after the removal of wave days (see text).
^b Classified according to their seasonal and geographical distribution in mainland California (see text).
^c Wilcoxon rank sum.
^d Sample size. Ranks of 0 are not included in sample.
^e Probability for two-tailed test.

test them. The first is that overall population levels have recently increased because of increased breeding success and/or increased winter survival. Most northern vagrant species, for example, originate from Canadian boreal forests east of the Rocky Mountains, and many have populations that fluctuate dramatically with the massive insect infestations that periodically occur there. There is an indication that larger than normal numbers of captures of some of these same northern vagrant species also occurred in the mid and late 1970's at certain eastern banding stations (D. Hussell pers. comm.). In addition, most vagrant species winter in the tropics, where they often prefer second growth or edge habitats rather than the

interior of mature forests (Willis 1966, Karr 1976). These forests are disappearing rapidly and are being replaced, in part, by fast-growing second growth or coffee and fruit plantations. The winter survival of certain of these North American migrants may recently have increased because of habitat changes favorable to them.

The second hypothesis is that some change in weather over an extensive area of the continent made the second 5 yr more favorable for weather-induced vagrancy, especially of northern species. Certainly, the 1974 fall invasion seemed well correlated with large-scale synoptic weather (Stallcup et al. 1975). In addition, unusual weather prevailed from 1975 to 1978

over much of the continent, with a succession of extremely hard winters in the northern, central, and eastern United States, and a 3-yr drought in California. These two phenomena were probably related, as both are to some extent caused by a displacement of the major persistent high- and low-pressure areas of the continent. The result was a flow of cold, moisture-laden air into the central and eastern United States from the north and northwest and a flow of dry, continental air into California from the northeast, a general weather pattern that also appears to be associated with large numbers of northern vagrants in California, at least in fall.

The two remaining hypotheses both involve an increase in the proportion of vagrant individuals in populations of these species. The first is that increased pesticide contamination on their tropical wintering ranges, and perhaps even on their breeding ranges, has recently increased the proportion of vagrant individuals. Able (1972) also speculated on the possible implication of toxic chemicals in the biosphere as a cause for the increased numbers of vagrants in recent years. While there is no good evidence linking pesticide contamination to orientation or navigation errors in birds, the possibility should not be unequivocally dismissed.

The final hypothesis involves a more general theoretical model that I am currently developing and testing. It is based upon the assumption that vagrants represent the extremes of dispersal (Grinnell 1922) and suggests that increasing rates of habitat change will selectively induce increasing amounts of dispersal in any population using that habitat. Habitat change is defined as the occurrence of a major physiognomic or specific change in the most important (in terms of density, dominance, and frequency) plant form occurring in any given area. Succession, as well as both natural and human-caused disturbance, therefore qualifies. The rate of change is expressed as the probability, P_h , that the habitat of any given area will change over time. Higher probabilities reflect greater rates of change. This parameter, P_h , is analogous to the inverse of Southwood's (1976) "duration stability" (H), the length of time that a particular habitat type remains in a particular geographic location.

The amount of dispersal can be characterized by the proportion, p_d , of dispersing individuals in the population. The model thus states that

as P_h increases, p_d selectively increases as well. If P_h for a given habitat is zero (the habitat is assumed never to change), dispersal should also be zero, because individuals optimally adapted to that habitat will be selected. If P_h is small, the amount of dispersal should also be small, but greater than zero, especially if habitat change is highly unfavorable or lethal to the population. Dispersing individuals will generally be selected against when no habitat change occurs, because they will most likely have a lowered probability of finding an equally acceptable habitat. They will be highly selected for when a habitat change does occur, however, because only they will have any probability of finding an acceptable habitat. If P_h increases further, it seems logical that p_d should also increase. Thus, the amount of dispersal in a population should selectively track the rate of habitat change to which that population is subjected.

As pointed out by Southwood (1976), organisms occupying relatively short-lived habitats tend to be exploiters or opportunists and lie toward the r -selected end of the r - K continuum. Relatively high amounts of dispersal will be a major component of their population process (Southwood et al. 1974). The model outlined here suggests that, as the rate of habitat change increases (habitats tend to become more short-lived), the amount of dispersal also increases (populations tend to become more r -selected). This is, of course, a gross oversimplification and neglects all other selective forces that could affect dispersal.

Increased dispersal in response to increased rates of habitat change need not be directly selected for in migratory landbirds. All that is needed is a weakening of the selection for accuracy of orientation or navigation. Thus, an increased proportion of vagrants and increased rates of range expansion would be expected in any migratory population in which dispersal is increasing. McLaren (1981) concluded that the apparent increase in vagrancy of certain species in Nova Scotia was related to the increased abundance and range expansion of these species rather than to "secular trends in the tendency of individuals to wander." I suggest that increased rates of range expansion and increased rates of vagrancy both could result from increased amounts of dispersal. Current field literature is replete with examples of recent range expansions. Whether the overall rate of range

expansion is actually increasing or the apparent increase is an artifact of increased observation awaits detailed study.

Without question, however, the rate of global habitat change has recently increased dramatically. Man's ability to alter the natural environment has attained monstrous proportions, and the recently increased number of vagrants on the Farallones may reflect a major underlying change in the dispersal characteristics of landbirds. This possibility enhances the importance of maintaining permanent stations for the long-term monitoring of bird migration. Southeast Farallon Island, because of its effectiveness in attracting and precipitating migrant landbirds, its small size, its relatively stable and unbiased sampling environment, and its effectiveness in sampling populations from virtually the entire North American continent, must continue to play a leading role in this monitoring.

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