

ORIGIN AND DIFFERENTIATION OF THE AVIFAUNA OF THE CHANNEL ISLANDS, CALIFORNIA

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The biota of the Channel Islands off the coast of southern California (fig. 1) for years has attracted the attention of evolutionists and biogeographers (Cockerell 1938). This interest focused in October 1965, when 102 participants convened at the Santa Barbara Botanic Garden for papers and discussion relating to the geology, biology, and archeology of the islands. Two years later, the results of the symposium were published (Philbrick 1967). Notably lacking among the several papers dealing with major vertebrate groups was an analysis of the resident avifauna of the islands; birds were mentioned only briefly in discussion following papers whose principal themes dealt with other topics.

In their patterns of distribution and differentiation, the land birds of the Channel Islands present a zoogeographic puzzle—complex enough to be fascinating, yet simple enough to encourage an attempt at solution. In this paper, I will review the kinds of differentiation shown by the endemic forms and will outline a general hypothetical model for the origin and course of evolutionary change in the avifauna considered in the light of information from geologic and paleobotanic history.

As Mayr (1943) demonstrated in a discussion of the origin of the birds of the Hawaiian Islands, remote island avifaunas are composed of elements which have accumulated from different sources and at different times. He viewed the land and fresh-water birds of the Hawaiian chain as having arrived via 14 separate invasions which could be grouped into seven levels of relative age, based upon their comparative degrees of morphologic change. Despite the fact that the Channel Islands, in contrast to the Hawaiian Islands, are only slightly removed from the North American continent and possess an avifauna with forms distinctive only below the species level, analysis of subtle patterns of distribution and of intraspecific variation provides a basis for the interpretation of probable routes of colonization and of stratification in age of the insular birds. In the discussion to follow I will at-

tempt to demonstrate that each species with a distinctive insular form has arrived in the Channel Islands at a different time and from a different source on the mainland. Furthermore, in a general review of the composition of the avifauna, I will discuss the species with undifferentiated island populations. Evidently, these species have not been present in the islands for a sufficient period of time to result in adaptive change and are considered to represent the most recently arrived forms. Finally, I will consider possible reasons for the absence, in seemingly appropriate habitat on the islands, of several species which occur commonly on the adjacent mainland.

MATERIALS AND METHODS

Information on morphologic divergence of the island birds, initially obtained from original descriptions and from subsequent systematic revisions where available, was verified by examination of study specimens in the Museum of Vertebrate Zoology, where are represented series of all of the insular subspecies as well as abundant material of their relatives from the adjacent mainland. Field experience on Santa Catalina and Santa Cruz islands was gained on visits in 1967. Nomenclature and sequence of species follow the Checklist of North American Birds (A.O.U. 1957), except that I recognize the endemic form of the Western Flycatcher (*Empidonax difficilis insulicola*) based on a revision nearing completion (N. K. Johnson, unpubl.). Only land birds will be considered in the present analysis; this category includes all species known to have evolved insular endemics.

In this paper the expression Channel Islands, or Santa Barbara Islands, will include the eight principal islands off the coast of southern California. The four Northern Channel Islands—Anacapa, Santa Cruz, Santa Rosa, and San Miguel—will be referred to as the “northern islands” or the “northern group.” The four Southern Channel Islands—Santa Barbara, Santa Catalina, San Clemente, and San Nicolas—will be referred to as the “southern islands” or the “southern group.”

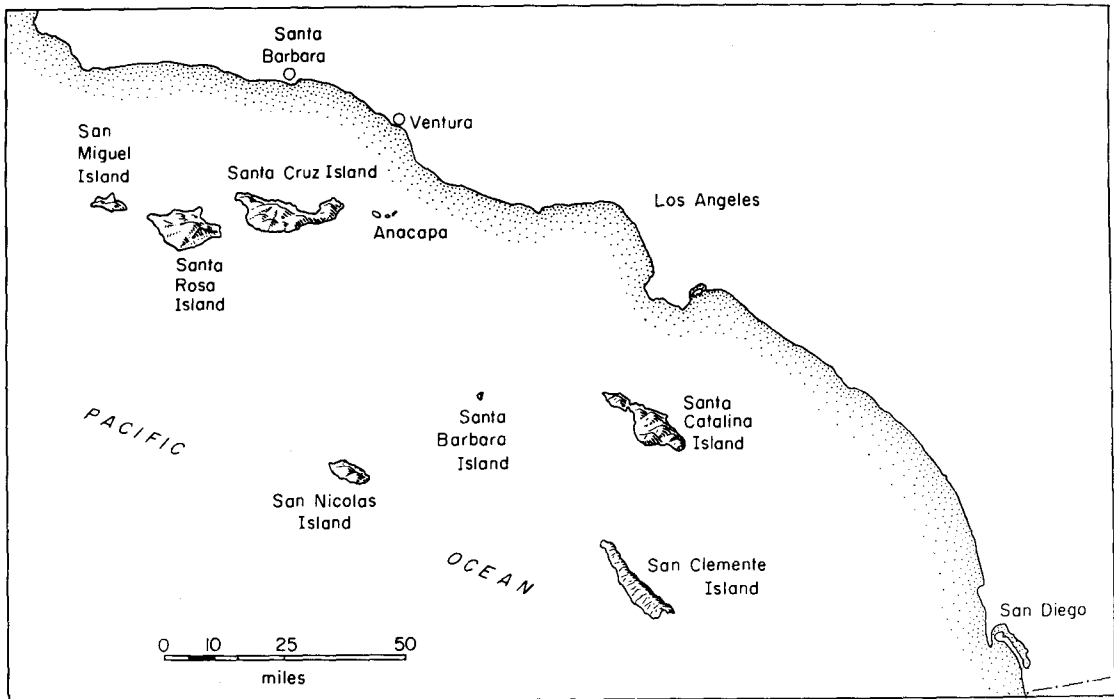


FIGURE 1. The Channel Islands, southern California.

There is currently available abundant literature on the Channel Islands which contains important papers on geologic and paleobotanic history. These papers are either contained in Philbrick (1967) or are cited in that volume. Of particular relevance to the present discussion are the papers by Axelrod (1967a and 1967b), Orr (1967), Valentine and Lipps (1967), and Weaver and Doerner (1967). Space does not permit even a cursory review of their findings here. However, in appropriate places in the text I shall cite information from these papers where it is crucial to the presentation of the story on avifaunal history.

SUBSPECIATION IN THE BIRDS OF THE CHANNEL ISLANDS

The pronounced differentiation of populations of birds in the Channel Islands has been appreciated since late in the 19th century. Although the present taxonomy is reasonably well advanced, two areas need further study: (1) additional examples of differentiation should be sought by refined analysis of adequate samples of forms now poorly represented by specimens (Red-tailed Hawk, *Buteo jamaicensis*; Saw-whet Owl, *Aegolius acadicus*; Bush-tit, *Psaltriparus minimus*; and Blue-gray Gnatcatcher, *Poliophtila caerulea*; among others); and (2) detailed interisland comparisons have yet to be made for several species

because samples from certain islands are insufficient. Notwithstanding the possibility of unrecognized yet significant variation, the degree of observed endemism is striking: 13 of 41 species (table 1), or 32% of the breeding land birds, show the effects of insular evolution. The fact that 9 of the 22 families (41%) of resident land birds represented contain endemic subspecies stresses the operation on the general avifauna of rather pervasive environmental influences, the results of which have transcended taxonomic boundaries.

THE DIRECTION OF DIFFERENTIATION

The trends of divergence of the island birds (table 2) show that selection has favored differentiation in a common direction for several characters. Fifteen of 18 forms (83%) are either darker (9 = 50%) or grayer (6 = 33%) than their relatives on the adjacent mainland, 13 of 18 forms (72%) have longer and/or heavier bills, and 9 of 17 forms (53%) have longer or heavier tarsi and/or feet. Lengths of wing and tail show no predominant trends of change in particular directions.

Howell (1917:16) was the first to point out that "the influences of this group of islands tend to produce a bird of greater total length, with larger, heavier bill, and heavier tarsus and foot. The length of wing and tail remains about the same, and coloration becomes darker, with brighter colors and heavier streak-

TABLE 1. The distribution of the endemic avifauna of the Channel Islands, California.

Species	Anacapa	Santa Cruz	Santa Rosa	San Miguel	Santa Barbara	Santa Catalina	San Nicolas	San Clemente	Subspecies on adjacent mainland ^e
California Quail (<i>Lophortyx californica</i>)	-	(intr.)	(intr.)	-	-	<i>catalinensis</i>	-	-	<i>californica</i>
Allen Hummingbird (<i>Selasphorus sasin</i>)	<i>sedentarius</i>	X ^b	X	-	-	X	-	X	<i>sasin</i>
Western Flycatcher (<i>Empidonax difficilis</i>)	<i>insulicola</i>	X	X	-	-	X	-	X	<i>difficilis</i>
Horned Lark (<i>Eremophila alpestris</i>)	<i>insularis</i>	X	X	X	X	X	X	X	<i>actia</i>
Scrub Jay (<i>Aphelocoma coerulescens</i>)	-	<i>insularis</i>	-	-	-	-	-	-	<i>californica</i> , <i>obscura</i>
Bewick Wren (<i>Thryomanes bewickii</i>)	<i>nesophilus</i>	X	X	-	-	<i>catalinae</i>	-	<i>leucophrys</i>	<i>correctus</i>
Loggerhead Shrike (<i>Lanius ludovicianus</i>)	<i>anthonyi</i>	X	X	-	-	X	-	<i>mearnsi</i>	<i>gambeli</i>
Orange-crowned Warbler (<i>Vermivora celata</i>)	<i>sordida</i>	X	X	X	X	X	-	X	<i>lutescens</i>
House Finch (<i>Carpodacus mexicanus</i>)	<i>frontalis</i>	X	X	X	<i>clementis</i>	X	X	X	<i>frontalis</i>
Rufous-sided Towhee (<i>Pipilo erythrophthalmus</i>)	-	<i>megalonyx</i>	<i>clementae</i>	-	-	X	-	X	<i>megalonyx</i>
Rufous-crowned Sparrow (<i>Aimophila ruficeps</i>)	<i>obscura</i>	X	-	-	-	- ^c	-	-	<i>canescens</i>
Bell Sparrow (<i>Amphispiza belli</i>)	-	-	-	-	-	-	-	<i>clementae</i>	<i>belli</i>
Song Sparrow (<i>Melospiza melodia</i>)	-	<i>clementae</i> ^d	X	<i>micronyx</i>	<i>graminea</i> ^e	-	-	<i>clementae</i>	<i>cooperi</i>
Total endemics:	7	10	9	4	4	9	2	10	

^a Not necessarily the closest relative of the endemic insular form. See text page 312.

^b X = the same subspecies occurs as is listed in the previous column.

^c Not reported since 1863.

^d a resident population may not be present on this island.

^e Presumed extinct.

TABLE 2. Direction of divergence of insular subspecies.^a

Island endemic	Color	Wing length	Tail length	Bill	Tarsus	Toes	Source
<i>Lophortyx californicus catalinensis</i>	D ^b	L	L	L,H	L	L	Grinnell (1906)
<i>Selasphorus sasin sedentarius</i>	*	L	-	L	-	-	Grinnell (1929)
<i>Empidonax difficilis insulicola</i>	Gr	L	L	L	L	L	Oberholser (1897); N. K. Johnson (unpubl.)
<i>Eremophila alpestris insularis</i>	D	S	S	L,Br	L	L	Townsend (1890); Behle (1942)
<i>Aphelocoma coerulescens insularis</i>	D	L	L	L	L	L	Henshaw (1886); Pitelka (1951)
<i>Thryomanes bewickii nesophilus</i>	D	-	S	-	-	-	Oberholser (1898); Miller (1951)
<i>catalinae</i>	D	-	-	L,H	H	L	Grinnell (1910); Miller (1951)
<i>leucophrys</i>	Gr	-	-	L	-	-	Anthony (1895)
<i>Lanius ludovicianus anthonyi</i>	D	S	S	L	-	-	Mearns (1898); Miller (1931)
<i>mearnsi</i>	D	S	S	S,H	-	-	Ridgway (1903); Miller (1931)
<i>Vermivora celata sordida</i>	D	S	-	L	L	L	Townsend (1890); M. F. McDiarmid (unpubl.)
<i>Carpodacus mexicanus clementis</i>	-	-	-	H	-	-	Moore (1939); Miller (1951); Power (1971)
<i>Pipilo erythrophthalmus clementae</i>	Gr	-	-	-	L	-	Grinnell (1897); Miller (1951)
<i>Aimophila ruficeps obscura</i>	D	-	-	H	L	H	Dickey and van Rossem (1923)
<i>Amphispiza belli clementeae</i>	-	-	-	L	-	-	Ridgway (1898)
<i>Melospiza melodia micronyx</i>	Gr	S	-	Li	Li	Li	Grinnell (1928)
<i>clementae</i>	Gr	L	L	-	L	L	Townsend (1890); van Rossem (1924)
<i>graminea</i>	Gr	S	S	Li	-	-	Townsend (1890); van Rossem (1924)

^a In each instance the comparison is with the subspecies resident on the adjacent mainland.

^b Br = broader; D = darker; Gr = grayer; H = heavier; L = longer; Li = lighter; S = shorter; * = differs in pattern on tail.

ing." Murphy (1938) also compared certain of the birds of the Channel Islands with mainland relatives and corroborated the finding of a general increase in bill size of the insular forms. The data of other authors, particularly Amadon (1953), Grant (1965), and Keast (1968), indicate that increased bill size is a commonplace insular phenomenon. In discussing the possible reasons for large general size in the island form of the Scrub Jay, Pitelka (1951:277) very early anticipated the view that the increase was permitted by relaxation of competition in simplified insular communities, when he stated that "large size

may be favored through differences in niche relationships of the island jay as contrasted with the mainland populations. Such differences would arise as a result of differences in the biotic structure of the two environments." Grant (1965) followed with the essentially similar conclusion that the bill is longer in island birds, allowing a greater range of food sizes on islands where species with similar ecologic requirements are often absent, and where certain of those species present are permitted to extend their activities to occupy at least portions of the vacant niches. The readily accessible birds of the Channel Islands would

seem to offer a fertile field for the examination and testing of these hypotheses.

Possible reasons for the longer tarsi of many island birds were explored also by Grant (1965, 1966), who concluded that the length of the tarsus is probably correlated with the nature of the perch and the way in which it is used. "Birds which feed and move on slender, not rigid, perches are likely to have a shorter tarsus than those which make a greater use of firm perches, in an upright posture" (Grant, 1965:360). Again, the Channel Islands birds should be examined quantitatively and be compared with relatives on the mainland for differences in niche use to ascertain the appropriateness of the above hypothesis.

Why have at least one-half of the endemic birds evolved darker plumages? Pitelka (1951: 271) seems to be the only author to comment in depth on this problem, in his discussion of the evolution of the race *insularis* of the Scrub Jay. His explanation was that winter predation by raptors might be reduced by blue coloration against a background of cloudiness and extensive fogginess together with the vegetational background. He also postulated a possible alternative, or additional, reason, that the Pleistocene vegetation inhabited by *insularis* was darker than that present now, and that the vegetation color became lighter, with increased aridity, while the darkness of the jay persisted. While both reasons also may explain the evolution of the dark plumages of the other endemic subspecies, I favor the hypothesis which stresses the matching of dark plumage coloration with the dark background of fog, vegetation, and perhaps soil of the insular environment. This explanation is at least in keeping with the generalization that dark plumages of birds commonly evolve in humid environments (Gloger 1833), and should suffice until more detailed data are available on the nature of the color adaptations in particular species.

Six island races of four species, the Western Flycatcher (*E. d. insulicola*), Bewick Wren (*T. b. leucophrys*), Rufous-sided Towhee (*P. e. clementae*), and Song Sparrow (*M. m. micronyx*, *M. m. clementae*, and *M. m. graminea*), are grayer than comparable mainland subspecies. This suggests that the evolution of these grayish races could have been related to more open and arid habitats of lighter, matching background colors than to habitats similar to those currently occupied by closely related forms on the mainland. All of these races except *micronyx* occur in the southern islands, and two are confined there. The cen-

ters of differentiation of the wren and the southern form of Song Sparrow were certainly in the more open and arid habitats of the southern group, on San Clemente and Santa Barbara islands, respectively. Did the gray races of the towhee and flycatcher, which occur on both northern and southern island groups, also evolve in xeric or semi-xeric habitats?

A clue bearing on this problem is found in the present habitat relations and relative numbers of Western Flycatchers on Santa Cruz, a well-wooded island of the northern group, compared with populations on Santa Catalina, a more arid island in the southern group. Contrary to expectation derived from experience with mainland forms of the Western Flycatcher, on the Channel Islands the species is most numerous and occurs in the greatest variety of habitats on Santa Catalina. This *Empidonax* is uncommon in woodlands on Santa Cruz, where one might expect substantial numbers. Perhaps in its abundant occupancy of open habitats on Santa Catalina, the grayish form of the Western Flycatcher reveals the general sort of environment involved in its evolutionary background. However, to suggest Santa Catalina as a likely island of origin for this form, because the present environment there is relatively open, would be improper. Of interest is the fact that the Western Flycatcher is the only grayish subspecies of Stratum II (see p. 309; table 4). It is also the only migratory species of this group. Therefore, selective pressure on this species to match the foggy winter background is presumably absent because the species apparently does not occur in the islands during that season. During the Xerothermic Period, arid habitats presumably extended over great parts of all of these islands, including Santa Cruz. It is likely, though, that total numbers of this apparently "arid-adapted" subspecies on Santa Cruz have diminished in the more moist and cool interval since the Xerothermic.

In the occurrence on Santa Rosa Island of gray races of towhee (*clementae*) and of Song Sparrow (*clementae*), and in the presence there of House Finches and Bewick Wrens with affinities toward populations on the southern islands (Miller 1951), one sees a significant faunal alliance of this island in the northern group to the southern, generally more arid islands. Perhaps San Miguel Island, where the grayish endemic *micronyx* of the Song Sparrow occurs, could also be included with Santa Rosa in this alliance. These facts, taken together with the past history of

profound aridity of Santa Rosa, suggest that during the Xerothermic there was a contrast, or important environmental break in addition to the obvious water barrier, between Santa Rosa and Santa Cruz. Santa Rosa evidently became very arid at about 2500 B.P. (Orr 1967:322). In contrast, Santa Cruz in its retention of the Scrub Jay and other faunal elements probably supported significant moist pockets, however local in occurrence, through even the driest part of the Xerothermic. The recognition of this environmental and biotic discontinuity in the northern group of islands will enable clearer interpretation of the present distributional patterns of the insular subspecies of birds.

COLONIZATION OF THE CHANNEL ISLANDS BY BIRDS

Geographic patterns of differentiation and distribution of the various forms in the islands (tables 1 and 2) provide evidence for several types of colonization to be discussed here; these categories are summarized in table 3.

In the following discussion, "single colonization" refers to the arrival and establishment for breeding of a species in the islands over a fairly narrow span of time, for example, a few months or even a few years. Arrival, establishment, and even interisland spread of several to many individuals of a species in the Channel Islands over a period of a few years is considered to be a "single colonization," because it is impossible to discern the sequence and relative spacing of each instance of arrival followed by breeding when these instances are closely spaced chronologically. An example is afforded by the invasion of the Red-breasted Nuthatch (*Sitta canadensis*) to the Farallon Islands off the coast of central California in 1969, where 311 individuals were banded between August and November 1969 (Point Reyes Bird Observatory 1970). This species did not settle in these islands, where suitable habitat for them is lacking, and therefore the example is not wholly appropriate, but this case does serve to illustrate the kind of events that might have led to what I would term a "single colonization," according to the usage of that expression in this paper.

By "multiple colonizations" I refer to the arrival, and establishment for breeding, of a species on two or more separate occasions, each of which is recognizably distinct because (1) the approximate times of arrival are actually known, as in the example of the Acorn Woodpecker which seems to have colonized the Channel Islands twice within the last 50 years

TABLE 3. Patterns of colonization of the Channel Islands by birds.

Single colonization from mainland (11 species)	
To Northern Islands:	
	Scrub Jay
	Rufous-crowned Sparrow
To Southern Islands:	
	California Quail
	Bell Sparrow
To Northern Islands ?, then interisland colonization:	
	House Finch → <i>clementis</i> line
	Western Flycatcher
	Horned Lark
	Allen Hummingbird → back to mainland
	Orange-crowned Warbler → back to mainland
To undetermined island, then interisland colonization:	
	Loggerhead Shrike → <i>anthonyi</i> line
	→ <i>mearnsi</i> line
	Song Sparrow → <i>clementae</i> line
	→ <i>micronyx</i> line
	→ <i>graminea</i> line
Multiple colonizations from mainland (2 species)	
I.	To undetermined island, then interisland colonization:
	Rufous-sided Towhee → <i>clementae</i> line
II.	To Santa Cruz Island:
	Rufous-sided Towhee → <i>megalonyx</i> line
I.	To Santa Catalina → Santa Clemente:
	Bewick Wren → <i>catalinae-leucophrys</i> line
II.	To Anacapa → Santa Cruz → Santa Rosa:
	Bewick Wren → <i>nesophilus</i> line

(see beyond); or (2) the resultant populations have attained such different degrees of adaptive change that different arrival times are indicated for each line. Indeed, the separate invasions may have occurred hundreds if not thousands of years apart.

SINGLE COLONIZATION FROM THE MAINLAND

In the endemic avifauna, 11 of the 13 species could have invaded the Channel Islands as a result of a single colonization from the coast of southern California. Within this group at least four subcategories can be distinguished.

1) *Species which colonized the Northern Channel Islands.* The Scrub Jay and the Rufous-crowned Sparrow occur at present only on certain islands in the northern group and there is no evidence that they ever bred in the Southern Channel Islands. Although J. G. Cooper supposedly collected two specimens of the latter species on Santa Catalina Island in 1863, there have been no subsequent records from there and I am inclined to feel that

these specimens were mislabeled in view of the circumstances surrounding a number of Cooper's records (Howell 1917:6, 80). The probable history of the jay will be discussed on page 307. The Rufous-crowned Sparrow presumably colonized Anacapa initially, then spread westward to Santa Cruz Island; it is now abundant on the latter island (Miller 1951). Oddly, this species was not known from Anacapa prior to August 1940, although it may have been overlooked previously (Banks 1966). Even if the first colonization of the northern islands involved birds which most likely used Anacapa as a steppingstone to Santa Cruz, the population on Anacapa may have died out there in the meantime only to reinvade during historic times, from the large population on Santa Cruz, by spreading eastward over water.

2) *Species which have colonized single islands in the southern group.* The California Quail and the Bell Sparrow belong in this category. As I will argue later in the paper, I believe that the quail on Santa Catalina Island resulted from an early introduction by prehistoric man. The Bell Sparrow, occurring only on San Clemente (the species may also occur on San Nicolas, but specimens from there have apparently not been preserved [Grinnell and Miller 1944:503]) probably colonized directly from the mainland by overwater waif dispersal. Whether it was once present on other islands in the southern group cannot be inferred from the evidence; however, the apparent confinement of this species to San Clemente Island does not require it.

3) *Species which may have colonized the northern islands then moved from there to the southern group.* The House Finch and the Rufous-sided Towhee are unique among the species which have evolved distinctive island subspecies in that the mainland form also occurs in the islands. In each species I think the mode of origin of this situation has been different; the finch arrived via a single colonization, the towhee via two invasions.

In the House Finch, the mainland race *frontalis* inhabits the northern group and *clementis* occurs on the southern islands, although as Miller states (1951:121) the populations on Santa Rosa and Santa Barbara Islands are somewhat intergradient. Power (1971) has demonstrated that even the Santa Cruz Island population of *frontalis* is slightly larger-billed and longer-legged than adjacent mainland birds, and therefore shows a weak approach to *clementis*. This situation may point to greater gene flow between the pop-

ulations of the northern islands and the birds of the mainland, perhaps because of their closer proximity. Although House Finches probably colonized the northern group first and then spread throughout the other islands, the distributional evidence is ambiguous and does not require this explanation; furthermore, habitat for this species is no closer on the mainland to the northern than to the southern islands. The House Finch could have arrived first on Santa Catalina, for example, then rapidly colonized the other islands from there, considering the substantial comparative vagility of this species. What the evidence does not favor is initial colonization of the southern group, then a period of divergence to form *clementis*, then range expansion into the northern islands where the populations are now intergradient because of interbreeding with the mainland populations. Indeed, I believe that after colonization and spread through the islands of the generalized mainland stock, environmental selection toward large bill size, on a north to south gradient starting in the northern islands (Miller 1951:121) and passing through well-defined *clementis* on San Clemente Island to finally culminate in heavy-billed *Carpodacus amplus* and *Carpodacus mcgregori* of Guadalupe Island and San Benito Island, respectively (Moore 1939), has probably resulted in the observed situation of distribution and morphologic divergence. In essence, this view has also been stated by Power (1971).

The Western Flycatcher, Horned Lark, Allen Hummingbird, and Orange-crowned Warbler each occur in the Channel Islands as strongly differentiated single races. What sort of colonization could have resulted in this pattern? These are species of either strong or substantial migratory tendency. Because no interisland subspeciation has occurred, we can assume that the local environments of individual islands do not exert sufficient selective pressure for such subspeciation or, if such pressure does occur, it is counteracted by substantial gene flow between islands which suppresses any emerging divergence. But the total influence on these species of the maritime environment must have been considerable to evolve the strong differences seen. As shown in table 3, I believe that the major colonizations and perhaps subsequent divergence of these species occurred in the northern islands and that interisland spread occurred fairly quickly and continues to occur.

4) *Species which colonized an undetermined island then spread among the islands.* For two

species which have evolved two or three moderately strong insular differentiates, the Loggerhead Shrike and the Song Sparrow, the sites of probable initial colonization in the islands are indeterminate. Both probably colonized the islands then spread to all but the outermost ones in the same general span of time prior to adaptive differentiation. Isolation in locally different insular environments then selected for the observed change. In the shrike, the ancestral stock probably established itself on all of the major inner islands, except for Santa Barbara. This stock then developed into *anthonyi*, except on San Clemente, where local selective forces acting perhaps in conjunction with the isolation of the island and on the genetic constitution of the founders produced *mearnsi*. There is no reason to assume that *anthonyi* and *mearnsi* have resulted from independent invasions from the mainland.

The present complex picture of distribution and differentiation in the Song Sparrow does not indicate that any of the insular races differ greatly in age, suggesting two or three invasions from the mainland, because all show approximately the same magnitude of differentiation. Although van Rossem (1924:219) stated that *graminea* was more strongly differentiated than *clementae*, before Grinnell had named the well-marked race *micronyx*, the complex sort of differentiation in several characters which is observed in these three races does not permit objective determination of degrees of adaptive change, and I prefer to consider them as all more or less equally divergent. Again in this example I conclude that the evidence points to the evolution of these grayish races from one generalized stock that invaded and spread to all the islands except San Nicolas. Different selective milieus on the various islands, probably during the early Xerothermic, guided the divergence of *clementae*, *micronyx*, and *graminea* as basically arid or semiarid-adapted, grayish subspecies of Song Sparrow. I suggest that these sparrows then died out on Anacapa and on Santa Cruz, on the latter island perhaps in response to unfavorable post-Xerothermic climatic and habitat changes and/or competition from the Rufous-crowned Sparrow. Miller (1951), in discussing the interesting possible inter-relationships in abundance and habitat preference of these sparrows on Santa Cruz and Santa Rosa, introduced the implicit notion of competition between them. The occasional occurrence of Song Sparrows of the race *clementae* on Santa Cruz Island I believe represents the results of colonization pressure from the dense

population on Santa Rosa Island to the westward, rather than a remnant population or a colonization from the population of *clementae* on San Clemente Island. This species is not known to breed on Santa Cruz, although it probably has done so at least rarely. Finally, the presence of Song Sparrows of the subspecies *clementae* on distant San Clemente Island argues for their probable past occurrence on Santa Catalina.

MULTIPLE COLONIZATIONS FROM MAINLAND

The Rufous-sided Towhee and Bewick Wren apparently have successfully invaded the Channel Islands on more than one occasion and evolved island endemics. A past double invasion can explain the present distributional picture in the Rufous-sided Towhee, in which the mainland race *megalonyx* breeds on Santa Cruz Island and *clementae* breeds on Santa Rosa, Santa Catalina, and San Clemente. I hypothesize an older invasion of pre-*clementae* to an undetermined island which spread through the islands in both the northern and southern groups, and a younger, fairly recent invasion of undifferentiated *megalonyx* stock to Santa Cruz. The latter invasion may have found the towhee niche unoccupied there or may have encountered a population of *clementae* which was absorbed or displaced. When Miller (1951:121) reported that the towhees of Santa Rosa Island were *clementae*, not *megalonyx* as mapped in Grinnell and Miller (1944:472), he called attention to a possible old line of approach between Santa Rosa and the southern islands which is suggested by the presence of a moderate submarine elevation. Evidence for the presence of a useful partial bridge here after early Pleistocene is weak (Valentine and Lipps 1967), and a bridge may not have existed at all.

As I indicated earlier, I believe that the alliance in the towhees, and in certain other subspecies, between populations on Santa Rosa and on the southern islands is likely a result of parallel evolution in similar xeric environments. It is improbable that *Pipilo e. clementae* on Santa Rosa was derived by invasion from either Santa Catalina or San Clemente Islands, or that *clementae* in the northern and southern islands evolved in parallel after separate invasions from the mainland.

In the Bewick Wren, the simplest explanation for the current distribution of the endemic insular races involves two distinct colonizations from the mainland. An older

invasion established a population on Santa Catalina, and, from there, birds reached San Clemente; this invasion was by birds ancestral to the *catalinae-leucophrys* line. Less strongly differentiated, and probably derived independently and more recently from mainland populations rather than from birds established on the southern islands, is the line which led to *nesophilus*. Birds ancestral to this line presumably spread first to Anacapa, then to Santa Cruz, and then to Santa Rosa. The species does not now occur on San Miguel. It may never have reached that distant island, or it may have been present in the past but died out. However, the low level of differentiation shown in the *nesophilus* line implies colonization of the northern group long after the connection with the land was severed, and after the invasion to Santa Catalina. Miller (1951: 120) commented on the origin of the Bewick Wrens of the northern group and reported minor color distinction, apparently indicating incipient subspeciation, of birds from Santa Cruz compared with those from Santa Rosa.

DOUBLE COLONIZATION WITHIN HISTORIC TIMES

In the group of undifferentiated species, the Acorn Woodpecker has apparently colonized the Channel Islands during the present century (Pitelka 1950; Miller 1955; Diamond 1969). This species represents the only colonist for which information on colonization is available and therefore the example is described in detail. Howell (1917) did not list the species in his summation of records for the islands up to that year. The first known occurrence was 2 and 3 April 1927, when Pemberton (1928) and party reported two individuals on Santa Rosa Island. Presumably this woodpecker had already arrived on Santa Cruz Island at the time of Pemberton's observations on Santa Rosa, and colonized Santa Rosa Island from there, because Hoffmann (1931) reported it from three widely separated points on Santa Cruz in 1930 and saw the species again in 1931. No further records from Santa Rosa have come to light and the species has apparently died out there. Although Miller (1951:122) listed the Acorn Woodpecker as present on both Santa Rosa and Santa Cruz Islands, his inclusion of Santa Rosa was apparently based on Pemberton's earlier report, for Miller did not find the species on Santa Rosa during intensive field work in March 1950, according to his careful field notes on file at the Museum of Vertebrate Zoology. On Santa Cruz Island the species was found again, in small numbers, by Pitelka (1950)

and by Miller (1951), and by May 1967, was abundant (N. K. Johnson, unpubl.).

In the Southern Channel Islands, the Acorn Woodpecker is known from only Santa Catalina where Miller (1955) reported several small groups of birds "spaced out over a mile of separate canyon systems" on 23 and 24 August 1955, in the oaks in Avalon and in the oaks in two canyons northwest of Avalon. By April 1967, the species had become abundant there (N. K. Johnson, unpubl.). It is not known when the species became established on Santa Catalina, but it could have been two decades or more after the colonization of Santa Cruz. This conspicuous species would not have escaped notice for too long in the vicinity of Avalon, an area visited frequently by naturalists. Furthermore, it seems most probable that the source of the colonizing birds on Santa Catalina Island was the large population on the mainland (20 miles distant), rather than the small population already breeding on Santa Cruz Island, 60 miles distant in the northern group of islands.

Therefore, the Acorn Woodpecker arrived overwater from the mainland to settle on Santa Cruz Island, perhaps in the 1920s, and from there colonized Santa Rosa Island, where the species has since died out. A second colonization from the mainland probably occurred during the late 1940s or early 1950s, to result in the establishment of the species on Santa Catalina Island.

Although the double invasion of the Acorn Woodpecker into the Channel Islands was presumably natural, it is difficult to assess the possible indirect role of man in habitat manipulation which may have led to an ecologic setting more favorable for the establishment of the species. Indeed, on Santa Catalina Island the bird seems commonest in introduced eucalyptus groves, and stores acorns abundantly in power poles and fence posts, additions to the habitat by man.

DISCUSSION

Although the present avifauna obviously represents the results of successful colonizations of species, it is likely that, in the long span of post-Pleistocene time, numerous other colonizations of the same species and of other species have also been successful, for brief periods, but have faded out. Diamond (1969: 62), for example, mentions that "the burrowing owl occurred on Anacapa before 1917, was still present in 1939, was absent in 1963 and 1964, present again in 1967, and had disappeared again by 1968." Such a mode of repeated arrival and die-off, if true, may be

quite common, especially among species on the smaller islands where low population sizes are probably typical. Therefore, I admit that a conspicuous difficulty arises in the assignment of "single" or "multiple" to the pattern of colonization of a particular species in view of the nature of the available data, and because of the manner in which species immigrate to islands near the continental shore.

Evidence that nine species (table 3) have probably sent successful immigrants first to the Northern Channel Islands is suggested by: (a) occurrence of the form only in the northern group; (b) similarity or identity of the race in the northern islands with that of the adjacent mainland; and (c) the habitat appropriate for many of the species on the mainland is closer to the coast at a position adjacent to the Northern Islands than to the islands of the southern group. Why have approximately twice as many colonizations started in the Northern Channel Islands than in the southern group? At least two reasons may be important: (1) The size of the combined area of the northern islands (195 square miles at present, and probably much larger at times in the past) plus the orientation of this chain in relation to the configuration of the adjacent coastline affords a broad front for the interception of migrants, particularly during the fall movement, when species populations are at annual highs and generally are heading southeastward. Diamond (1969:61) has stated essentially the same view. However, his generalization (Diamond 1969:61-62) that, "The island distances are also small compared to the dispersal powers of California resident species which undertake radial postbreeding wanderings rather than north-south migrations" is incorrect, except for a few species. Many of the resident birds in California are strictly sedentary, insofar as is known, and a number of species in this group are the conspicuous absentees in the island avifauna. (2) Anacapa, at 13 miles offshore, is the closest island (actually, Anacapa is a group of three small islands) to the mainland of any of the eight islands here considered and therefore could serve as a convenient steppingstone to any of the other three large islands situated immediately to the west. Not only would the combined area of the northern group favor colonization, but differentiation as well could have been promoted on this relatively large area after the arrival of small pioneer stocks.

Diamond (1969:61), in discussing the apparent lack of influence of distance from the mainland upon avifaunal turnover rates of

the individual Channel Islands, had hypothesized that "dispersal distances of the bird species that colonized the islands are large compared to the distances of the Channel Islands to the mainland (up to 61 miles)—i.e., a potential colonist leaving the mainland, *if capable of dispersing over water at all* (italics mine), has almost as good a chance of reaching the farthest island . . . as the nearest island." In essence I agree with this view. When one considers the species of both regular migrants and vagrants that have been recorded from the Channel Islands, even with vastly insufficient study, then the numbers and variety of potential colonists must be enormous.

Is the proposed outline of major post-Pleistocene trends in routes of colonization and local extinction invalidated by Diamond's (1969) claim of very high rates of extinction and colonization in the islands? Do on-going changes distort the distribution patterns beyond recognition, obliterating the opportunity to decipher the histories of these patterns? I do not think so for several reasons, one of which is that high avifaunal turnover in the Channel Islands has not been proved. Granted that insular species turnover is probably higher than that of continental habitats of comparable size, Diamond's figures for turnover rates in these islands are unacceptable because of the nature of the avifaunal records from which they were calculated. A more detailed evaluation of his turnover rate figures will be presented elsewhere (J. F. Lynch and N. K. Johnson, in prep.).

Furthermore, I feel that Diamond vastly underestimates the influence in the islands of man and his animals in habitat modification which has permitted colonization by some species and caused the extinction of others. Many of the range adjustments and faunal changes within the last 100 years are probably the result of habitat changes wrought by human agricultural and livestock practices occurring in recent, historical times, long after the original waves of colonization established the birds in the islands and permitted their differentiation as endemic races thousands of years ago. Banks (1966) has documented the kind of historical changes in the habitats and avifauna of Anacapa resulting from relaxation of intensive grazing there by sheep. In recent years two species (Rufous-crowned Sparrow and Chipping Sparrow) of shrubland habitats have strikingly increased in numbers as the shrubby vegetation of the island recovered. Two other species (Horned Lark and West-

ern Meadowlark) dependent upon the open grassy habitats perpetuated by the former grazing have shown a remarkable decline in numbers as their preferred habitat diminished. Faunal changes of this sort, resulting from relatively recent habitat modifications by man and his introduced animals, should not qualify for inclusion in discussion of long term natural cycles of colonization and extinction of components of insular faunas.

However, extinction and interisland colonization are probably still altering in a minor way the distributions of many of the species with endemic races. Cycles of recolonization would be expected which would send individuals to small islands (or to small areas of habitat) from centers of abundance on large islands (or in large areas of habitat), after die-off on the former as a result of normal fluctuations in numbers. I stress "interisland colonization" because many colonizations (or recolonizations) probably involve birds from other insular populations in the Channel Islands group, individuals already with island adaptations. New colonizations from the mainland, which would more seriously confuse an attempted reconstruction of the distributional picture, probably occur in far lesser frequency. Thus, if the Scrub Jay sends colonists from Santa Cruz Island to Santa Rosa Island (which it probably does, rarely), and if the Rufous-crowned Sparrow occasionally sends colonists in the opposite direction, from Santa Cruz to Anacapa, these minor changes should not invalidate the general hypotheses presented earlier (p. 300 ff) about the original prehistoric routes of colonization of these forms from the mainland. Specimens of recent colonists, especially where they represent species with distinctive island forms, are urgently needed to aid in the testing of this assumption. One recent example supports this postulate, that of the apparent recolonization of Anacapa by the Rufous-crowned Sparrow. Importantly, the seven specimens Banks (1966: 183) mentions are all of the race *obscura*, the insular endemic form existing in large numbers on Santa Cruz Island, the probable source of the colonists to Anacapa rather than the mainland where two other subspecies breed.

SIMILARITY OF COASTAL MAINLAND POPULATIONS TO THE ISLAND ENDEMICIS

In several species, populations along the coast of southern California show phenotypic approach or identity to the endemic island subspecies. This could result from one or more

of the following causes: (1) parallel evolution of coastal mainland and insular stocks under the influence of similar maritime environments; (2) actual gene flow from the island populations to the mainland populations; and/or (3) establishment on the mainland by invasion of the insular endemic. Furthermore, (4) island populations of certain forms show evidence of gene flow from the mainland to the islands. As illustrated diagrammatically in figure 2, examples of all four phenomena can be seen among the birds of the Channel Islands.

Parallel evolution of coastal mainland and insular stocks under similar maritime environments. The Loggerhead Shrike (fig. 2a) is illustrative of this situation, as explained by Miller (1931:82). Extreme coastal *gambeli* "show a partial resemblance to *anthonyi*," the race which occurs on all of the northern islands except San Miguel and on Santa Catalina Island. Miller doubted "that shrikes regularly pass from the Santa Barbara Islands to the mainland or vice versa inasmuch as the island populations are extremely uniform and apparently receive no dilution as a result of invasions by *gambeli*. Furthermore, no specimens entirely typical of *anthonyi* are to be found in the extensive representation of birds from southern California. The similarity of some mainland birds to *anthonyi* is due, probably, to a set of environmental conditions along the mainland shores, which are similar to conditions on the island and which operate upon island and mainland birds in like manner. Mainland birds thus modified by these conditions fail to establish a colony of *anthonyi*-like individuals because they are not isolated from the large inland population. The possible rare or occasional passage of *anthonyi* to the mainland could not account for the repeated occurrence of intermediates along the beaches of southern California."

Gene flow from the islands to the mainland. The Horned Lark (fig. 2b) may illustrate both the first and, especially, the second phenomena. This species regularly migrates from the islands to the seaboard of the mainland where some individuals could remain to breed (Grinnell and Miller 1944:268-269). However, there remains some doubt as to the relative roles of parallel evolution versus gene flow from the islands because in coastal mainland *actia*, "all manner of intergrades are present between these extremes [of *insularis*] and birds typical of *actia*," and "there remains the possibility that such mainland examples resembling in-

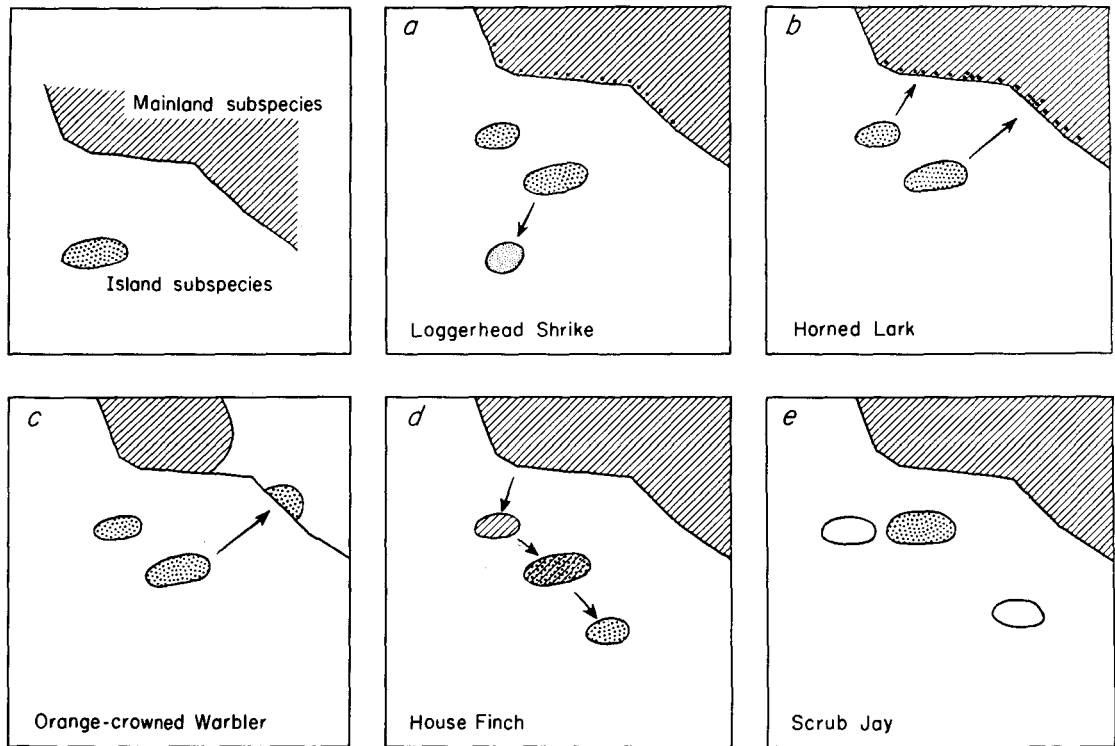


FIGURE 2. Generalized schematic distributions and probable patterns of gene flow between mainland populations and the insular subspecies. (a). Loggerhead Shrike. Gene flow rare or absent between populations on the islands and on the mainland, but coastal mainland examples of *gambeli* resemble *anthonyi* in the islands, presumably as a result of parallel evolution. The probable derivation of *mearnsi* (fine stipple) from *anthonyi* (heavy stipple) is indicated by the arrow. (b). Horned Lark. Some gene flow from islands to the mainland, but apparently not in the reverse direction. (c). Orange-crowned Warbler. Invasion of mainland by insular endemic after evolution on the islands. No known gene flow on mainland between the two subspecies. (d). House Finch. Gene flow from mainland to the northern islands, and/or increasing selection pressure for divergence (increasing bill size) toward the southern islands. (e). Scrub Jay. Relict pattern of distribution in the northern islands, with no gene flow between populations on Santa Cruz Island and mainland.

sularis may be extremes of *actia*" (Behle 1942: 260-262).

Recolonization of the mainland by insular endemics. This phenomenon is shown by two species, the Orange-crowned Warbler (fig. 2c) and the Allen Hummingbird. In both species, colonies of the island subspecies exist in pure form on the coast of the mainland and, importantly, in isolation from mainland populations representing other races. The most clearly documented example is that of the Orange-crowned Warbler (*V. c. sordida*) which breeds in two restricted areas along the coast, between Redondo and San Pedro in Los Angeles County, and in the vicinity of San Diego (Grinnell and Miller 1944:395), despite the presence at 20 miles to the north and perhaps closer, in the Santa Monica Mountains, of *V. c. lutescens* in apparently pure form (Miller 1946). Almost certainly the mainland was recolonized from Santa Catalina, the island adjacent to the northern coastal mainland colony, which supports a denser

population of this warbler than any of the other Channel Islands. It is important to note that *sordida* apparently has not expanded its range beyond the immediate coast. It is unknown whether *lutescens* was displaced from the local coastal habitat by *sordida*, when the latter arrived, or whether the coastal habitat favored by *sordida* was open for colonization because it was unsuitable for *lutescens*. In view of the current gap separating the ranges of *sordida* and *lutescens* on the mainland, and because of the distinctly maritime habitat occupied by *sordida* there, I favor the second alternative.

The reinvasion of the mainland, also near San Pedro, by the insular form *sedentarius* of the Allen Hummingbird has occurred only recently and is currently under study by Shirley Wells and Gary Stiles. As in the example of the warbler, the colonists probably originated on adjacent Santa Catalina Island where the species is abundant. The nominate race occurs on the immediate coast of the main-

land south definitely to the vicinity of Morro, San Luis Obispo County and probably to Santa Barbara and Ventura counties, although the records from the latter areas are questionable (Grinnell and Miller 1944:222). *Selasphorus sasin sasin*, therefore, may occur as close as approximately 60 miles northwest of the colony of *sedentarius* near San Pedro. This example also serves to indicate that the insular form is not as sedentary as previously had been believed.

Gene flow from the mainland to the islands. The occurrence in the islands of the mainland subspecies of the House Finch (fig. 2d) and the Rufous-sided Towhee has already been discussed. A further example pointing to gene flow from the mainland to the islands is in the Allen Hummingbird, in which species intermediates between *sasin* and *sedentarius* are known from Anacapa Island, an appropriate place for such to occur in view of the geographic position of this island between the main ranges of the two subspecies (Grinnell and Miller 1944:222). Also, in the Western Flycatcher, spectrographic analysis of vocalizations (N. K. Johnson, unpubl.) reveals that a peculiar inflection of the position note is more accentuated in the population on Santa Catalina Island than in birds from Santa Cruz Island at a position closer to the mainland. It remains obscure whether this implies increased gene flow from the mainland to Santa Cruz Island, versus lesser gene flow to the southern islands, or greater selective pressure for the occurrence of this modified vocalization in the population from Santa Catalina. Although this situation might suggest that the populations of the Western Flycatcher in the moist canyons near the Santa Barbara coast are influenced by interbreeding with *E. d. insulicola* from the islands, the three specimens available from the coastal mainland adjacent to the islands show no signs of morphologic intermediacy with the island bird. However, the population in the Santa Barbara area is isolated; San Ardo, Monterey County is the southernmost positive locality near the coast to the north of the Santa Barbara population, and the latter population could indeed have some genetic contact with the insular birds in view of their proximity.

RELATIVE TIMING OF THE COLONIZATIONS: STRATIFICATION OF THE AVIFAUNA

In the previous section I developed an hypothetical explanation of the probable routes of colonization and subsequent spread through the islands of the ancestors of the present en-

demic forms. That analysis was founded principally on evidence from insular distribution patterns and geographic trends in morphologic change, both evaluated in terms of their relationship to the geographic variation and location of source stocks on the mainland. Now I wish to supplement these same lines of evidence with information on magnitude of divergence, the latter interpreted in the light of the tendency of the mainland populations of the species (a) to subspeciate, and (b) to migrate, wander, or disperse, that is, their relative vagility (table 4). This will permit the development of a model of the timing of the colonizations. A synthesis of these kinds of information permits an interpretation of the meaning of the morphologic variation shown and, therefore, provides the basis for a speculative assessment of the length of time each form has been in the islands. Furthermore, such an analysis should be viewed against a setting of the probable geologic and geofloral history of the islands, taking into consideration what is known of the habitats occupied by the various species. I assume two things: (1) the general habitat preferences of the species involved have not changed greatly over the span of time necessary for the evolution of the insular endemics; and (2) in view of the levels of divergence attained and considering the geologic history of the islands, we are dealing with relatively young patterns of evolution, partly late Pleistocene but mainly post-Pleistocene in age.

The breeding avifauna can be sorted into five categories of differentiation which outline in general terms the relative lengths of time each species has occurred in the Channel Islands (table 4). This arrangement, although admittedly speculative, is in keeping with the facts of the history of the islands and of the differentiation and distribution of the birds that occur there.

Stratum I—Old peninsular relict. Scrub Jay. The endemic insular race of this species, found at present only on Santa Cruz Island (fig. 2e), has been the focus of much discussion in the literature (Henshaw 1886; Dawson 1920; Pitelka 1951; Miller 1951; Howell and Raven, in Philbrick 1967:90-91). Most authors have simply expressed surprise at the absence of this jay from Santa Rosa Island, where perfectly suitable habitat seems to exist (Miller 1951), but have not commented further about matters of distribution or of origin.

In view of the degree of differentiation attained, the race *insularis* of the Scrub Jay has been in the Channel Islands longer than any

TABLE 4. Categories of differentiation and faunal stratification among the birds of the Channel Islands, California.

	Number of differences ^a	Other races in California ^b	Relative vagility ^c
<i>Stratum I—Old peninsular relict</i>			
1. Scrub Jay (Santa Cruz Island)	6	6	1
<i>Stratum II—Strong differentiation, single races</i>			
2. Orange-crowned Warbler (7 islands)	5	2	5
3. Horned Lark (8 islands)	6	7	3
[4. California Quail (Santa Catalina Island)] ^d	6	3	1
5. Western Flycatcher (5 islands)	5	2	5
6. Allen Hummingbird (5 islands)	3 ^e	1	5
<i>Stratum III—Moderately strong differentiation, multiple races</i>			
7. Song Sparrow (3 races on 5 islands)	4-5	11	1
8. Loggerhead Shrike (2 races on 5 islands)	4	3	2
9. Bewick Wren (pre- <i>catalinae-leucophrys</i> line)	2-4	6	2
<i>Stratum IV—Weak differentiation, single races</i>			
10. Rufous-crowned Sparrow (2 islands)	4	2	1
11. Rufous-sided Towhee (pre- <i>clementae</i> line)	2	5	1
Bewick Wren (pre- <i>nesophilus</i> line)	2	—	2
12. House Finch (8 islands; endemic race on 4)	1	1	3
13. Bell Sparrow (San Clemente Island)	1	3	2
<i>Stratum V—Undifferentiated species^f</i>			
Anna Hummingbird	—	0	3
Saw-whet Owl	—	0	3
Rock Wren	—	0	3
Bush-tit	—	3	1
Acorn Woodpecker	—	0	2
Rufous-sided Towhee (<i>megalonyx</i> line)	—	—	1
<i>Absentees^f</i>			
Screech Owl	—	7	1
Nuttall Woodpecker	—	0	1
White-breasted Nuthatch	—	3	2
Wren-tit	—	4	1
Plain Titmouse	—	6	1
California Thrasher	—	2	1
Brown Towhee	—	6	1

^a Based on the categories in table 2.

^b From Grinnell and Miller (1944).

^c Subjective estimates of relative development of migratory or nomadic tendency among mainland relatives in California: 1, low; 2, moderately low; 3, medium; 4, moderately high; 5, high.

^d Probably introduced.

^e Tarsus and middle toe measurements not included because of the great difficulty of measuring these in hummingbirds.

^f List incomplete.

of the other species that have evolved island endemics. Because of the sedentary nature of this species I am not surprised at the lack of Scrub Jays on Santa Rosa Island, located only 5 miles from a population estimated at 2000 to 3000 pairs (Dawson 1920:28; Pitelka 1951:276) on Santa Cruz. What is difficult to explain is the presence of this species on any of the Channel Islands via overwater crossing. I propose that the most convincing explanation of the current distribution assumes that this jay colonized overland, during the peninsular

stage of the northern group of islands in the Pleistocene, and that subsequent habitat modification in response to climatic change has restricted a former more general distribution in the Northern Channel Islands to Santa Cruz. There seems to be no reason to believe that the Scrub Jay did not once occur on Santa Rosa Island, where a forest of *Cupressus* with trees up to at least 2 ft in diameter was present at 16,000 B.P. in a wet and cool climate (Orr 1967). Furthermore, the presence of Douglas fir on Santa Cruz at 14,200 B.P. (Chaney and

Mason 1930), at a time when all of the northern islands were connected, argues for the occurrence of the jay on Santa Rosa at least when it was better wooded than at present. Presumably the jay died out on Santa Rosa sometime after 7500 B.P. when the climate was drying rapidly and becoming more desert-like. Orr (1967:322) describes and documents further drying and dune building on Santa Rosa between 4000 and 3000 B.P. "which probably eliminated all but a few relict forests of the Highlands. The drying period continued, and by about 2500 B.P. . . . the Indians had almost completely ceased to use acorns or seeds as food." These statements indicate exactly the kind of detrimental habitat changes that would have influenced any population of jays on Santa Rosa—the diminution or elimination of cool temperate forests of oaks. Even with the partial recovery of appropriate habitat during the increasingly temperate climate of post-Xerothermic times (Axelrod 1967b), evidently the highly sedentary tendencies of the Santa Cruz stock have not permitted the overwater "recolonization" of Santa Rosa to the present day.

Stratum II—Strong differentiation, single races. The Horned Lark, Western Flycatcher, Orange-crowned Warbler, and Allen Hummingbird have each evolved (1) highly distinctive insular representatives, with (2) only one race in the islands per species, which (3) each occur on from five to eight of the Channel Islands. In addition, a number of other shared attributes suggests that all four of these species may have arrived via overwater movement in the same general span of time, the cool-moist period between the end of the Pleistocene and the beginning of the Xerothermic; (4) all are species of an ancestry which probably involved moist forest or moist woodland edge, as is well described by Behle (1942:301-303) for the form *insularis* of the Horned Lark, a race most closely allied to *strigata* of the grassy openings in humid coastal forest of western Washington and Oregon. (5) All are species of moderate to high degrees of vagility (table 4), and, except for the Horned Lark (the least vagile of the four), show no great proclivity to form races. This suggests that their strong differentiation is significant and reflects comparatively long isolation. Their moderate to strong migratory tendencies indicate that, although potential and/or actual swamping from mainland stocks may be substantial, they are able to maintain their distinctive insular features. Finally (6) at least two of these species, the hummingbird and the warbler,

have recolonized the mainland, and the other two may interbreed with mainland stock at least rarely, if not occasionally. The latter point indicates the substantial relative population sizes of the species in this stratum and implies, in at least the two species that have definitely reinvaded the mainland, an unusual degree of dominance (in the sense of Darlington 1957:24) in these insular differentiates.

Within the four species of this stratum, it is not possible to clearly identify early or late colonists, although one could speculate that the species most clearly associated with forests (Western Flycatcher) and clearings in forests (Horned Lark) arrived before those associated with woodland edge and wet chaparral (Orange-crowned Warbler and Allen Hummingbird).

One other species of this general category, the California Quail, has evolved a strongly characterized race found only on Santa Catalina Island. Discussion of this form will be deferred until the end of this section because of the special nature of this example.

Stratum III—Moderately strong differentiation, multiple races. The Song Sparrow, Loggerhead Shrike, and Bewick Wren (*precatalinae-leucophrys* line) form a group of species that share the following characteristics: (1) well-defined, but not striking, differentiation in the islands; (2) interisland subspeciation of two or three races per species; (3) residence on five islands; (4) ancestors which probably preferred savanna or brushland-chaparral; (5) moderate to strong tendency to subspeciate on the mainland; and (6) low or moderately low levels of vagility in mainland races. Also (7) two of the species, the sparrow and the wren, seem to have become established in the islands as a result of more than one colonization. These two species also seem to form subspecies rapidly, presumably a result, in part, of their strongly sedentary behavior. For this reason I do not think that their level of differentiation attained in the islands (three races for each species) suggests that they have been there for a greater period of time than the species of Stratum II, which are more resistant to race formation. On the basis of the magnitude of variation shown by the insular endemics of the three species in this group and in view of the general sort of habitat occupied, I feel it is highly probable that these species arrived after those in Stratum II, perhaps in the early phases of the Xerothermic Period, or even more recently.

Stratum IV—Weak differentiation, single races. The Rufous-crowned Sparrow, Rufous-

sided Towhee (*pre-clementae* line), House Finch, and Bell Sparrow seem to form the youngest group of species in the Channel Islands that have evolved insular subspecies. The *pre-nesophilus* line of the Bewick Wren also belongs here. They share the following characteristics: (1) comparatively minor differentiation; (2) an ancestry involving a preference for brushland and/or grassland-opuntia habitat; (3) low to moderate tendency to subspeciate; and (4) low to moderate vagility. Two of the species, the towhee and the finch, share the distinction of the presence in the islands of both the mainland subspecies and the insular endemic. The Rufous-crowned Sparrow seems to be the most strongly divergent form of the group and is placed at the head of the list. These species may have arrived in the Channel Islands in the Xerothermic or post-Xerothermic Period, in view of the magnitude of their divergence and their general habitat preferences.

Stratum V—Undifferentiated species. This group of species, several of which are listed in table 4, is composed largely or entirely of forms which I assume have colonized the Channel Islands most recently; apparently they have not had sufficient time to develop distinctive traits in the insular environment. The Acorn Woodpecker is an example of an undifferentiated species that has become well established on at least two of the islands during the present century. Although their period of isolation has been too short to result in adaptive change, the characteristics of the insular populations should be carefully studied when the accumulation of samples permits detailed analysis of morphologic variation. Certain species in this stratum, for example, the Bush-tit, may be categorized as "undifferentiated" because adequate samples of specimens necessary to demonstrate possible differentiation are not yet at hand. Furthermore, some species included here may be undifferentiated not because they are recent arrivals in the islands but for the reason of their resistance or inertia (homeostasis) to phenotypic change. The Anna Hummingbird (*Calypte anna*) may be such a species; it has not subspeciated in its limited range in California and Baja California, even though it is essentially permanently resident. The occurrence of this hummingbird on several of the Channel Islands, and on Guadalupe Island to the south, where Howell and Cade (1954) report birds with possible difference in vocalizations from mainland birds, argues further for the presence of the species in the islands for

a substantial period of time, and for arrival via overwater crossing. The fact of differentiation in the islands of several other species with substantial inertia to evolutionary change (Stratum II) suggests that the presence of the Anna Hummingbird in the islands certainly does not antedate the species of Stratum III or, perhaps, even those of Stratum IV. The situation remains puzzling and the interpretation ambiguous; indeed this species may have colonized the islands very recently, even within historic times.

The Bush-tit, a species of low vagility and moderate subspeciation in California (table 4), occurs in undifferentiated form (as far as known) on Santa Cruz and Santa Catalina Islands. In view of its sedentary habits and weak flight, the presence in the islands of this species is most difficult to explain. During three-fourths of the year, the species forms flocks, commonly of from 15 to 20 individuals (Grinnell 1903). The species is of very light weight for a songbird (4-6 g). I hypothesize that small groups of Bush-tits from the dense populations on the mainland may have been blown to the islands and have become established in appropriate habitat. Their absence on Santa Rosa Island in the apparently suitable oak-chaparral only 6 miles from a population of low to moderate density on Santa Cruz may be a fortuitous result of colonization overwater by waifs.

Absentees. A number of authors have commented on the imbalance of the breeding avifauna of the Channel Islands when compared with that of the adjacent mainland (Pitelka 1951; Diamond 1969). A list of the missing species includes many of the most typical birds of Californian oak woodland and chaparral (table 4). If the Northern Channel Islands were connected to the mainland at some time in the Pleistocene, then why are these species missing from present-day vertebrate communities on the islands?

Two possibilities, both unlikely in my opinion, are apparent: (1) all species reached the Channel Islands over water. The conclusion of the geologists that a land bridge existed (an opinion reached independently of faunal information) makes this point seem spurious. (2) The absentees colonized over the land bridge along with the jay, but all but the jay died out. This notion is improbable in my opinion, because I do not consider the jay to have had a dry oak woodland-chaparral ancestry. I believe instead that its background was associated with a situation of wet and cool Pleistocene forest or forest edge. The

dark plumage of the jay is in keeping with this view (see p. 299). If any species died out after crossing the Pleistocene land bridge, they would have been boreal birds (see beyond), not dry oak-chaparral forms.

I suspect that the most probable reason for the absence of the dry oak-chaparral species is the likelihood that the habitat was unsuitable for their occurrence during the period of connection with the mainland. Indeed, according to the descriptions (Axelrod 1967b) of late Pleistocene and post-Pleistocene floras from coastal southern California, habitats near the coast on the mainland may also have been unsuitable, with the nearest populations located more interiorly. Evidently it was only after the land connection was broken, when boreal habitats receded to the north and were replaced by more temperate or even xeric vegetation, that many of the species currently absent from the islands occurred coastally on the mainland. Why did not some of them then cross the water barrier to colonize the islands as have so many other species?

The absentees are all species which are permanently resident in chaparral and oak woodlands of coastal and central California. They are among the most sedentary species in the country and totally lack any migratory movements (table 4). Presumably, they are also species that show great reluctance to cross water. Evidence for this point is found in the summary of banding operations on the Farallon Islands, located 19 miles off the coast of central California, which summary was reported by the authorities of the Point Reyes Bird Observatory (1970). The species which are listed as absentees in the Channel Islands have never appeared on the Farallon Islands despite the fact that the list of species recorded from the latter islands, as a result of a major banding program, is extensive and includes a number of very unlikely visitors. It is of interest that the Scrub Jay, a species that in my opinion has not colonized the Channel Islands via overwater movement, has been recorded from the Farallon Islands (Gruber 1884:172). Pitelka (1951:220-221, 272) discusses this record; he has informed me (pers. comm.) that he now feels that this bird was a vagrant and the result of accidental transport to the island, perhaps by ship.

There is another group of absentees that deserves at least passing comment. Almost certainly during the period of the extensive occurrence of closed cone pine forest southward along the California coast and over the Channel Islands (Axelrod 1967a), there were species

of boreal birds present which now do not occur because the closed cone pine forest is too limited in extent or is otherwise unsuitable. Many or most of these species would have died out during the Xerothermic Period, when boreal conditions were most restricted, and have failed to recolonize the more appropriate cool temperate habitat which was available after the termination of the Xerothermic. Hairy Woodpeckers (*Dendrocopos villosus*); Pigmy Nuthatches (*Sitta pygmaea*), a species highly adapted to bishop and Monterey pine on the mainland (Norris 1958:127); Red-breasted Nuthatches (*Sitta canadensis*); Red Crossbill (*Loxia curvirostra*); and some form of *Junco*, among other widespread species of boreal derivation, probably occurred in the Channel Islands in the earlier moist period but have since died out. Although the Red-breasted Nuthatch and Red Crossbill still occur at least sporadically, and may occasionally breed, I suspect that substantial populations of both species were present during cool and moist post-Pleistocene times. The genus *Junco*, which has successfully colonized Guadalupe Island where a distinctive species evolved, doubtless bred formerly on the Channel Islands.

Introduced differentiate? The above analysis includes all of the endemic subspecies of the Channel Islands birds with the exception of the distinctive form *catalinae* of the California Quail on Catalina Island. Grinnell (1906) argued strongly that this race was native on Santa Catalina. The degree of distinction attained in both size and in color by the insular population makes it seem unlikely that the quail on Santa Catalina were introduced, at least within historic times. Natural overwater colonization by rafting is an unlikely possibility, in view of the prevailing ocean currents, and flight by this species directly to the islands from the mainland is out of the question. I propose that the quail were introduced on Santa Catalina Island by Indians, who have been in the islands for at least 12,000 years and possibly much longer (Orr 1967:320-321). The quail may have been brought for food although there is no evidence on this point. In any event, even an introduction only a few centuries ago could have resulted in strong differentiation in view of current findings of rapid evolutionary rates in introduced species (Johnston and Selander 1964). Evidence for a possible late Cenozoic connection of Santa Catalina Island to the mainland is not at all convincing (Valentine and Lipps 1967), and if such a connection were present in the

past which permitted passage by quail. I am at a loss to explain the absence on Catalina of a host of other vertebrate species which presumably could have colonized in the same fashion, but evidently did not.

THE ISLAND ENDEMICS:
RELICTS OR INSULAR
DIFFERENTIATES *IN SITU*?

In common with many other authors (Cockrell 1938; Philbrick 1967), I am concerned with the broader aspects of the evolution of the endemic biota of the Channel Islands. The endemic forms could represent either survivors on the islands as relictual populations of species of more widespread former distributions, or populations which have diverged in the islands after colonization from stocks on the adjacent mainland. Relict forms which demonstrate the first alternative are well known in the insular floras (e.g., species of *Lyonothamnus*, *Quercus*, and *Pinus*, among others; see LeConte 1887; Axelrod 1967a, 1967b; Muller 1967) and in the island herpetofauna (e.g., *Batrachoseps relictus* and *Klauberina riversiana*; see Brame and Murray 1968; Savage 1967). Raven (1967) implies that both alternatives may be indicated by the insular species of plants when he states that the floras "of San Clemente and Guadalupe islands consist of mixtures of various elements present on the mainland in the past, as well as distinctive endemics that may have evolved *in situ*."

The avifauna of the Channel Islands also may be composed of both relictual elements and insular differentiates. Subspecies of at least two species, the Scrub Jay and the Horned Lark, could be of relictual origin, although I believe that in both examples there is evidence that insular adaptation has occurred subsequent to the initial isolation of the island populations. In a previous section, I hypothesized a course of events which could have led to the present confinement of the race *insularis* of the Scrub Jay to Santa Cruz Island, after contraction of a former range through the northern islands. Such a distributional history alone qualifies the island jay as a "relict"; indeed, that is how I categorize it (table 4). But can we find evidence for an even more widespread past distribution which also included continental populations? In his detailed examination of geographic trends in color and size in all forms of *Aphelocoma*, Pitelka (1951) sought close relatives for *insularis* from among mainland subspecies, but except for establishing the alliance of *insularis* with the subspecies group "*californicum*," he

found no near relationships. The example remains problematical; in view of the relatively great age of this form in the Channel Islands, *insularis* could be remnant of a long extinct mainland representative of *Aphelocoma*, which occupied extensive habitat of moist woodland and forest edge in the Pleistocene, and which was displaced by the northward progression of vigorous, more arid-adapted races as drying ensued. On the other hand, there may never have been a former mainland stock similar to present day *insularis*; in the direction of evolution toward large size of bill and tarsus and in dark plumage, this race may represent nothing more than the extreme in a common pattern of insular differentiation widely shown by many of the endemic forms of birds occurring in the Channel Islands, differentiation which was arrived at solely by evolution in isolation in the islands.

The Horned Lark provides a more convincing illustration of relictual distribution. In this species, Behle (1942) postulated that the subspecies *insularis*, presently occurring in the Channel Islands, forms a phyletic unit with two other heavily pigmented, yellowish forms, *sierrae* of conifer-bordered meadows in the northern Sierra Nevada, and *strigata* of grassy openings in the moist, forested Pacific region of western Washington and Oregon. Presumably, this ancestral line enjoyed a widespread past distribution in openings in the extensive late Pleistocene forest of *Pseudotsuga*. Increasing aridity in post-Pleistocene times fragmented the originally broad range and the distributional gaps were filled in part by northward spread of races of the *rubea-actia-ammophila* line (Behle 1942:301-305). Although *insularis* is appropriately considered a relict form surviving in the islands, with its closest relative, *strigata*, currently found many miles to the north along the northwest coast, there is no reason to assume that *insularis* has not differentiated somewhat as the climate became more arid and habitats were correspondingly altered in the islands after the Pleistocene. In this sense, then, the island race of the Horned Lark could be thought of as both a Pleistocene relict and an insular differentiate. The fact of the existence of insular adaptations in *insularis* versus *strigata*, by the shorter wing, longer tarsus, and longer middle toe of the former race, points to the high probability of some degree of adaptive change in *insularis* since the ancestors of this form first arrived in the Channel Islands.

Three other species may have been in the islands for a period of time sufficient to show

relictual patterns of evolution, the Orange-crowned Warbler, Western Flycatcher, and Allen Hummingbird. Of these, only the warbler suggests a relictual distributional situation in that *sordida* may be more closely related to the race *orestera* of interior and northern boreal habitats than to *lutescens* of the Pacific coastal area, including the mainland immediately adjacent to the Northern Channel Islands. An analysis of geographic variation in this species, currently being pursued by M. F. McDiarmid, may throw light on the relationships of the several races.

SUMMARY

Of the approximately 41 species of land birds which breed in the Channel Islands, California, 13 (32%) are represented by 18 endemic subspecies. When compared with their relatives on the adjacent mainland, these endemic forms are characterized by darker or grayer coloration, longer and/or heavier bills, and longer and/or heavier tarsi and toes.

Eleven of these 13 species could have invaded as a result of a single colonization; two species, the Rufous-sided Towhee and the Bewick Wren, have apparently arrived twice, with each of their immigrations separated by long spans of time. Colonizations probably occurred either directly to the Northern Channel Islands, directly to the Southern Channel Islands, or initially to the Northern Islands followed by movement to the southern group. For three species, the site of first colonization is indeterminate. The Allen Hummingbird and Orange-crowned Warbler have reinvaded the coastal mainland after evolution in the islands. Limited gene flow in the Horned Lark occurs from the islands to the mainland, whereas in the House Finch the gene flow seems to be in the reverse direction. In the Loggerhead Shrike, some coastal mainland birds apparently have evolved in parallel with the insular subspecies.

Geologic and paleobotanic evidence from the northern Channel Islands indicates a mid-Pleistocene connection with the mainland, then later isolation by water. During this period, the habitats varied from Boreal, through the late Pleistocene, to warm-arid, during the Xerothermic Period, to cool temperate at present. A hypothetical model based on evidence derived from degree of differentiation, habitat preference, tendency to subspeciate, and relative vagility of the species from which the endemic forms were derived, accounts for the origin of the present avifauna.

Several species, all common residents of mainland Californian chaparral and oak woodland, are conspicuously absent in the islands even though appropriate habitat seems to occur. These species are unusually sedentary on the mainland and are very poor overwater colonists. Their absence on the islands is attributed to the likelihood that habitats were unsuitable for their overland colonization during the period of the land connection in the mid-Pleistocene.

As is indicated by certain other elements of the insular biota, the endemic avifauna in the Channel Islands of California contains examples of subspecies which show relictual patterns of evolution and distribution as well as races which have undergone their entire divergence as a consequence of insular isolation.

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DEDICATION

This paper is dedicated with respect to the memory of Professor Loye H. Miller, ornithologist and paleontologist, who counseled emerging naturalists to appreciate biotic and geologic events of the past, thereby to gain clearer insight into the evolution of definitive complex communities.

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