Breeding Land Birds of the Channel Islands

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INTRODUCTION

Biologists are familiar with the thought that islands have unique scientific value as natural laboratories where the mainland species pool is reshuffled by differential immigration, extinction, and evolution to form new communities of fewer species. As material for studying these natural experiments, birds of the Channel Islands are of special interest. The reason for this interest is not that the birds themselves are unique: Channel Islands birds are far less distinct than those of the Galapagos (*e.g.*, see Power 1980), and they are also less distinct than the Channel Islands plants that Philbrick (1980) has discussed. But birds are the most easily observed, best-studied organisms on the Channel Islands, and hence they are the organisms for which we have the most detailed information on ecological topics such as population dynamics, niche shifts, and competition.

WHAT BIRD SPECIES ARE ON THE CHANNEL ISLANDS?

Table 1 summarizes the status of all breeding land bird species on the eight Channel Islands. Included in the table are the 56 species of birds that do not normally alight on water and that are known to have bred on at least one or more of the Channel Islands. Several additional species, including the Great Blue Heron and Cooper's Hawk (formerly on Santa Cruz), the Sora (Santa Cruz, 1936), the Common Poor-will (Santa Catalina), Lawrence's Goldfinch (occasionally on Santa Rosa), and the Red Crossbill, Lark Sparrow, and Dark-eyed Junco (occasionally on Santa Cruz), may breed occasionally, but convincing evidence is lacking. For a discussion of marine birds on the Channel Islands, see Hunt *et al.* (1980). Published general papers dealing with birds of the Channel Islands are those by Howell (1917), Grinnell and Miller (1944), Diamond (1969), Johnson (1972), Power (1972, 1976), Yeaton (1974), Lynch and Johnson (1974), Jones (1975), and Jones and Diamond (1976). Many other papers dealing with individual islands are cited in these references.

What breeding land bird species are found in island habitats, compared with similar mainland habitats? Many familiar mainland species are present in the same habitats on the islands, such as the Horned Lark in open grassland. Some common mainland species, such as the Wrentit, which is so abundant in mainland chaparral, are completely absent on islands with suitable habitat. Still other mainland species (*e.g.*, the Orange-crowned Warbler and Rock Wren) are greatly increased in abundance or occupy a wider range of habitats on the islands. In all, each island supports between eight and 39 breeding land bird species—far fewer than the 160 species that breed on the adjacent southern California mainland. Fifty-six land bird species have been documented as breeding on one or more islands (Table 1), and nearly 200 other species have been recorded from the islands as migrants, winter visitors, or vagrants.

All these species can be assigned to a list with eight categories, depending on the species' patterns of breeding and occurrence on the islands:

(1) Some species of the adjacent mainland never breed on the islands and have never been recorded on the islands, not even on a single occasion as a vagrant. This list of absentees includes sedentary mainland species that are the commonest species in chaparral: Wrentit,

TABLE 1. Breeding land birds of the California Channel Islands (total of 56 species).

Species	San Miguel	Santa Rosa	Santa Cruz	Anacapa	San Nicolas	Santa Barbara	Santa Catalina	San Clemente
Red-tailed Hawk	O	rB	rB	O			rB	O
Bald Eagle	E	E	E	E	E	E	E	E
Osprey					E	O?	E	E
Peregrine Falcon	E	E	E	E		E	E	E
American Kestrel	rI	rB	rB	rB	O	O	rB	rB
California Quail							rB	
American Oystercatcher			rI					
Black Oystercatcher	rB	rB	rB	rB	O	rB	O	O
Killdeer		rI	rI				rI	
Snowy Plover	rB	rB	?		rB			?
Rock Dove							rB	
Mourning Dove		rB	rB	O			rB	rB
Barn Owl	rB	?	rB	rB		rB	?	rB
Burrowing Owl	E or O	rB or O	rB or O	?	O	rB	rB	rB or O
Long-eared Owl							O	
Saw-whet Owl			rB				rB	
White-throated Swift		rB	rB	rB			rB	rB
Costa's Hummingbird	O?					O		
Anna's Hummingbird			rB				rB	O
Allen's Hummingbird	rI	rB	rB	rB			rB	rB
Common Flicker			rB				rB	
Acorn Woodpecker			rI				rI	
Ash-throated Flycatcher			sI					
Black Phoebe		rB	rB	O			rB	O
Western Flycatcher		sB	sB	sB			sB	sB
Horned Lark	rB	rB	rB	O or E	rB	rB	rB	rB
Barn Swallow	sB	sB	sB	sB	O	O	sB	sB
Scrub Jay			rB					
Northern Raven	E	rB	rB	O	rB	E or O	rB	rB
Bushtit			rB				E	
Red-breasted Nuthatch			O					
Bewick's Wren		rB	rB	rB			rB	E
Rock Wren	rB	rB	rB	rB	rB	rB	rB	rB
Northern Mockingbird		rB	rB	O	O		rB	rB
American Robin			O					
Swainson's Thrush							O	
Blue-gray Gnatcatcher			rB					
Phainopepla							O	
Loggerhead Shrike	O	rB	rB	O		O	rB	rB
European Starling	rI	rI	rI	rI	rI	rI	rI	rI
Hutton's Vireo		rB	rB	O			rB	
Orange-crowned Warbler	rB	rB	rB	rB	rI	O	rB	rB
House Sparrow		E			rI		rI	rI
Western Meadowlark	rB	rB	rB	rB	rI	rB	rB	rB
Red-winged Blackbird			O					
Hooded Oriole							O	
Brewer's Blackbird					O			
Black-headed Grosbeak			sI					
House Finch	rB	rB	rB	rB	rB	E	rB	rB
Lesser Goldfinch	O	O	rB				rB	
Rufous-sided Towhee		rB	rB				rB	E
Rufous-crowned Sparrow			rB	rI or O				
Sage Sparrow								rB
Chipping Sparrow		sB	sB	sI			sB	sB
White-crowned Sparrow					O			
Song Sparrow	rB	rB	rB			E		E

B= breeds every year.
O= has bred on one or more occasions, but not every year.
I= has immigrated and become an established breeder.
E= formerly bred but has not bred recently (extinct).
?= breeding status unclear.
r= present year round (permanent resident).
s= present during the breeding season only.

Brown Towhee, California Thrasher, Plain Titmouse, and Nuttall's Woodpecker. This list also includes some strong overland fliers like the Red-shouldered Hawk, Turkey Vulture, Black-chinned Hummingbird, and American Goldfinch, which simply refuse to cross water and are seldom or never recorded on the islands. The Common Crow is another strong flier that refuses to cross water and is rarely recorded, unlike its relative, the Northern Raven, which has bred on all eight islands. These species do not breed on the islands because they cannot or will not fly there.

(2) There are two species that do breed on a single island as a native, endemic subspecies but for which there are no historical records of individuals dispersing to or between islands: the Scrub Jay and California Quail. These are sedentary species that somehow reached an island by a rare chance event in the distant past (Wenner and Johnson 1980).

(3) Many species occur abundantly on the islands at some season but never breed because the islands do not offer the appropriate breeding habitat. This category includes numerous Sierran coniferous forest species, such as the Hermit Thrush and Fox Sparrow, which are common winter visitors on the islands.

(4) Some species occur rarely on the islands (or on some particular island) and do not breed, despite the presence of suitable habitat, because the occasional individual that reaches an island does not find a mate there. For instance, Cañon Wrens rarely reach the islands. A single Cañon Wren has been present on Santa Cruz Island since at least August 1973, without a mate having arrived.

(5) Several species reach the islands in numbers every year and find suitable breeding habitat there, but nevertheless do not breed. These species present one of the most puzzling problems in the Channel Islands avifauna. Examples of such species are the House Wren, Warbling Vireo, Northern Oriole, Ash-throated Flycatcher, Black-headed Grosbeak, and Brown-headed Cowbird, which flood the islands in spring migration each year. None bred on the islands until the Ash-throated Flycatcher and Black-headed Grosbeak recently began breeding on Santa Cruz Island, although they are still not breeding in similar and equally suitable habitats on Santa Catalina and Santa Rosa. Our guess is that these are highly philopatric species which tend to return each year to the mainland area where they were born, even if they migrate through other areas with similar habitat.

(6) Several species reach the islands but breed rarely or only in low numbers, evidently because of competition from a related species. For example, Anna's Hummingbird breeds in low numbers on two islands, was once recorded breeding on a third island, and has been recorded from other islands only as a vagrant, yet it is an abundant breeder in similar mainland habitats. We attribute its rareness as a breeder on the islands to competition from the abundant insular populations of Allen's Hummingbird.

(7) Numerous species reach islands where they breed in some years but not in other years. For example, a pair of Northern Mockingbirds bred on San Nicolas in 1968, but not in 1969, 1970, or 1971, bred again in 1972, not in 1973, and bred in 1974, 1975, and 1976. There are many similar cases of bird species that breed on a particular island on this sporadic basis.

(8) Finally, there are dozens of species that breed on some particular island every year (*e.g.*, the Rock Wren and House Finch on Santa Catalina).

DYNAMICS OF LAND BIRD POPULATIONS

The breeding bird fauna of an island is not fixed forever but changes, often from year to year, as local populations immigrate and die out. The word "turnover" is used to refer to these changes in local species composition. It is an important general problem in population biology to estimate turnover rates and to estimate population lifetimes. These rates surely differ among islands and among plant and animal groups. The rates are of theoretical interest to biologists, and of much practical interest to conservationists.

To measure turnover rates in Channel Islands bird species, one of us (J.M.D.) carried out breeding bird surveys on the islands in 1968, and the other of us (H.L.J.) began doing annual breeding surveys in 1973. In these surveys, we have been helped by many resident and visiting observers on the islands. Our goal was to obtain virtually complete lists of the breeding bird species on each island in successive years. A detailed account of our methods has already been published (Jones and Diamond 1976). We shall only mention briefly here that we have developed efficient survey procedures to reduce the chance of overlooking breeding populations and to prove, by finding nests, eggs, or fledglings, that species observed were actually breeding. We have calculated turnover conservatively; the numbers given below may slightly underestimate actual turnover rates. For comparison, we shall cite qualitatively similar but much more detailed results from breeding surveys on European islands (Diamond and May 1977, Reed 1977). For example, on some European islands it is known not only which species bred but also how many pairs of each species bred in each year for the past several decades.

Turnover rates T for the Channel Islands have been calculated from surveys conducted between 1973 and 1977 (from 1972 for Santa Barbara Island) and computed as: $T = 100(I + E)/(S_1 + S_2)(t)$ where I and E are the number of species that immigrated and went extinct, respectively, between two survey years; S_1 and S_2 are the number of breeding species present in the first and second survey years, respectively; and t is the time interval (in years) between surveys. In most instances, $t = 1$ (surveys conducted every year); in a few instances, however, $t = 2$ when we failed to obtain a complete survey in a given year, as on Santa Catalina in 1974. For example, the average yearly turnover rate ($\overline{T}$) for Santa Catalina is 1.8 per cent per year, computed as follows:

1973-1975	$100(0 + 1)/(33 + 32)(2) =$	0.8
1975-1976	$100(2 + 0)/(32 + 34)(1) =$	3.0
1976-1977	$100(1 + 0)/(34 + 35)(1) =$	1.5
		5.3 $\overline{T} = 5.3/3 = 1.8$

The average yearly turnover rates (per cents) for the other islands are: Santa Barbara, 5.6; Anacapa, 3.0; San Miguel, 2.2; San Nicolas, 5.7; San Clemente, 2.4; Santa Rosa, 0.6; Santa Cruz, 1.3.

Figure 1 illustrates the detailed population fluctuations revealed by the annual breeding surveys of European islands, in this case on the British island Calf of Man. Qualitatively similar fluctuations have been observed for Channel Islands bird populations, although the available data are less dramatic because fewer survey years and less precise breeding population estimates were available. In Figure 1, the fluctuations in breeding populations of four ground-dwelling species in consecutive survey years from 1959 to 1974 are shown. The uppermost depicted species, the Wheatear, did not breed in the first survey year, 1959; one pair bred in 1960; none bred in the next three years; one pair bred in 1964; two bred in 1965; none bred in 1966; and from 1967 the population gradually crept upwards from two pairs and then fluctuated between five and eight pairs. Between 1959 and 1974 the Wheatear immigrated three times and disappeared twice on Calf of Man. Had the censuses been made on the island only in 1959 and 1974, one could have concluded that there had been only a single case of turnover and a single immigration (because the species was absent in 1959 and present in 1974); one would have been unaware that two additional immigrations were offset by two extinctions in the intervening years.

The next species depicted in Figure 1, the Stonechat, bred in good numbers from 1959 to 1962, until the harsh winter of 1963 eliminated the whole population. Not until 1965 did a

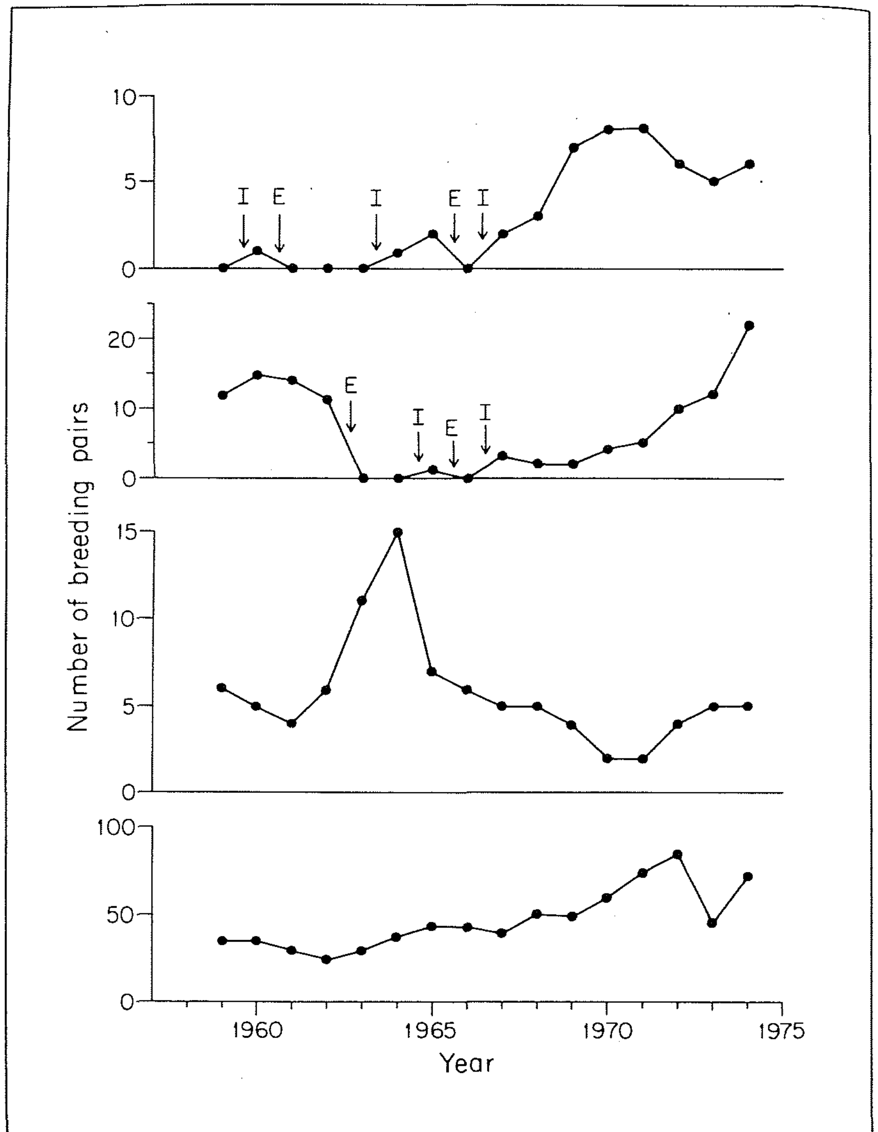

FIGURE 1. *Number of breeding pairs of four ground-dwelling bird species on Calf of Man, a small British island in the Irish Sea, as revealed by annual breeding censuses from 1959 to 1974. From top to bottom the species are: Wheatear, Stonechat, Skylark, and Meadow Pipit. An arrow marked* E *indicates an extinction of a local population (*i.e., *an instance in which there was a breeding population one year but not in the succeeding year). An arrow marked* I *indicates an immigration (*i.e., *an instance in which there was a breeding population in one year but not in the preceding year).*

single pair again breed. The pair did not return in 1966, but in 1967 breeding resumed with three pairs, gradually increasing to 22 pairs by 1974. Had only the censuses of 1959 and 1974 been available, one would have concluded that the Stonechat did not turn over on Calf of Man, since it bred in both census years. One could not have guessed that four cases of turnover had occurred in the intervening years: two extinctions reversed by two immigrations.

The two remaining species shown in Figure 1, the Skylark and Meadow Pipit, bred in every survey year and exhibited no turnover. Nevertheless, their populations went through large fluctuations, especially in the case of the Skylark, which ranged from two to 15 breeding pairs and came close to disappearing in 1970 and 1971.

We have observed numerous similar cases of population fluctuations for Channel Islands birds. The on-again, off-again breeding of the one or two pairs of Northern Mockingbirds on San Nicolas between 1968 and 1976, already mentioned, resembles the fluctuations in the Wheatear on Calf of Man between 1959 and 1967. House Finches on Anacapa have gone through large fluctuations in recent years that, at one point, reduced the population to four breeding pairs but did not quite produce an extinction; this is similar to the history of the Skylark on Calf of Man. As is true for the Meadow Pipit on Calf of Man, the Northern Mockingbird and Orange-crowned Warbler on Santa Rosa have gone through large population fluctuations, but the population has always remained large enough that it was not in danger of extinction.

Figure 1 emphasizes one of the main practical problems in turnover studies. If the available information consists only of a pair of surveys spaced many years apart, one is likely to underestimate turnover because of immigrations offset by subsequent extinctions (or *vice versa*) in the intervening years. That is, breeding populations appear and disappear repeatedly between survey years. Figure 2 depicts the magnitude of error that this sporadic breeding introduces into turnover studies. The British island of Lundy was surveyed almost every year from 1922 to 1974. We have calculated turnover from all pairwise combinations of censuses and plotted the apparent turnover rate as a function of the number of years between censuses. For example, turnover at a 20-year interval was calculated by comparing the species lists for 1949 and 1969, or 1950 and 1970, or 1951 and 1971, *etc*. The true turnover rate for Lundy calculated from censuses at one-year intervals is 9.4 per cent per year. That is, every year, on the average, 9.4 per cent of Lundy's breeding populations fail to survive until the next year and are replaced by a similar number of new breeding species that did not breed in the previous year. With an increasing interval between surveys, the apparent turnover rate plummets and is 1 per cent per year or less for survey intervals of 23 years or more. Even for a census interval of three years, the apparent turnover rate is barely half of the true value. We previously published a figure analogous to Figure 2 depicting the decline in apparent turnover rate with increasing census interval for Anacapa, one of the Channel Islands (Jones and Diamond 1976).

All of the several dozen European islands that we have analyzed, and all eight Channel Islands, exhibit this drastic decline in the apparent turnover rate with increasing census interval due to sporadic breeding. Census intervals of a decade or more underestimate the turnover rate by about an order of magnitude. The true turnover rates, based on one-year intervals, range from less than one to nearly six per cent per year for the Channel Islands, and from two to twenty per cent per year for islands of northern Europe.

Figure 3 summarizes our turnover results for the eight Channel Islands. This figure depicts the fluctuations in breeding species number for each island, based on all years since 1897 for which adequate breeding surveys were available. Three conclusions can be drawn from the figure. (1) Species number is not fixed on each island, but fluctuates as populations immigrate and go extinct. For example, the number of species breeding in a given year fluctuates on Santa Cruz from 35 to 39; on Anacapa, from 15 to 19; on San Nicolas, from 8 to 12. These

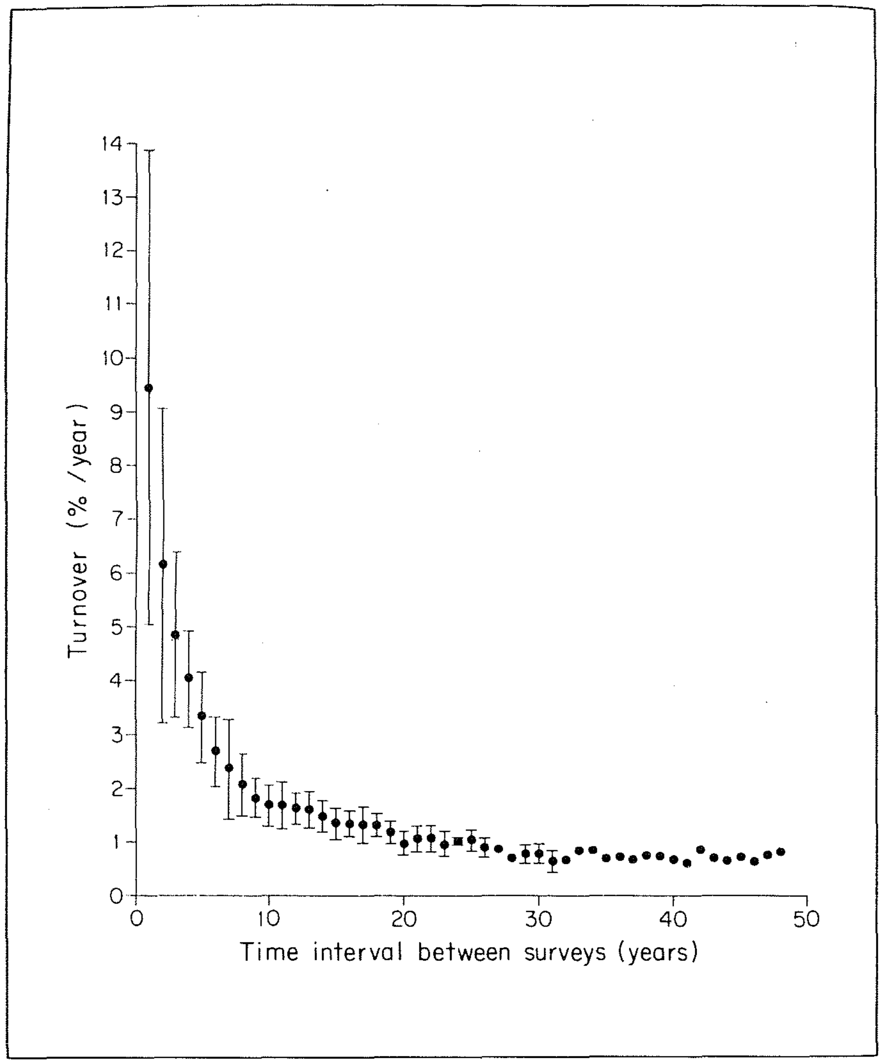

FIGURE 2. *Apparent turnover rate of the breeding land bird community on the British island of Lundy as a function of time interval between surveys. Lundy has been surveyed nearly annually from 1922 to 1974. For each pairwise combination of census years, turnover (in units of per cent/year) was calculated as* $100(I + E)/(S_1 + S_2)t$, *where* I *is the number of apparent immigrations and* E *the number of apparent extinctions revealed by comparison of species lists for the two years:* S_1 *and* S_2 *are the numbers of breeding species in the earlier and later census years, respectively; and* t *is the number of years between censuses. The calculation was carried out for all pairs of census years corresponding to a given time interval; the resulting average value and standard deviation of the turnover rates were plotted as the solid point and vertical bars, respectively.*

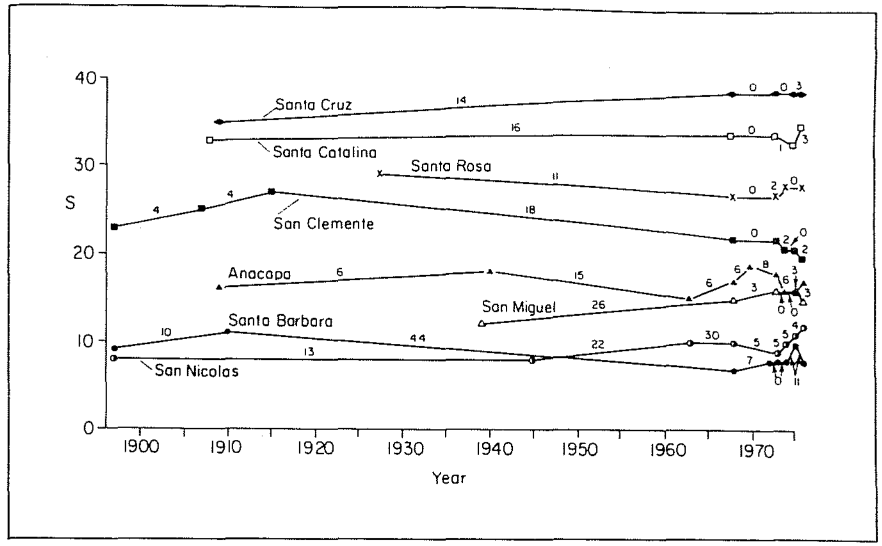

FIGURE 3. *Turnover and fluctuations in breeding species number on the Channel Islands. For each Channel Island, and for each year since 1897 in which the number of breeding land bird species (S) was adequately determined, S is plotted on the ordinate against the survey year on the abscissa. The number on the line connecting each pair of censuses is the absolute turnover in units of per cent of the island's breeding species turning over between surveys:* i.e., $100(I + E)/(S_1 + S_2)$; *see legend of Figure 2 for explanation of these symbols.*

fluctuations remain within modest limits unless island habitats are much altered, as happened on Santa Barbara between the 1910 and 1968 surveys (Philbrick 1972). Thus, the number of breeding species on an island is set by a dynamic equilibrium between immigrations and extinctions. (2) The numbers on the line connecting each pair of points in Figure 3 represent the absolute turnover (percentage of island species turning over between surveys), *not* the turnover rate in per cent per year. A zero means that there was no turnover. It can be seen that between most survey years there is some turnover, even in one-year periods. (3) There can be turnover even if species number remains constant. This occurs if the number of immigrations happens to equal the number of extinctions. For example, on San Nicolas between 1963 and 1968, the number of breeding species remained constant at 10, but turnover was 30 per cent because three populations disappeared and three new ones immigrated.

What populations turn over? As illustrated by Figure 4, the populations most prone to extinction are smaller populations: species such as big raptors with large territories, species living in specialized habitats, or any species on a small island. In Figure 4, we have grouped Channel Islands bird populations by the approximate number of breeding pairs and calculated for each group the fraction of the populations in the group that disappeared during the time that surveys have been made. It will be seen that no population exceeding 1,000 pairs has disappeared and that nearly half of the populations numbering just a few pairs have disappeared. The larger a population, the lower its probability of extinction and the longer its probable lifetime. There are also characteristic differences between species in proneness to

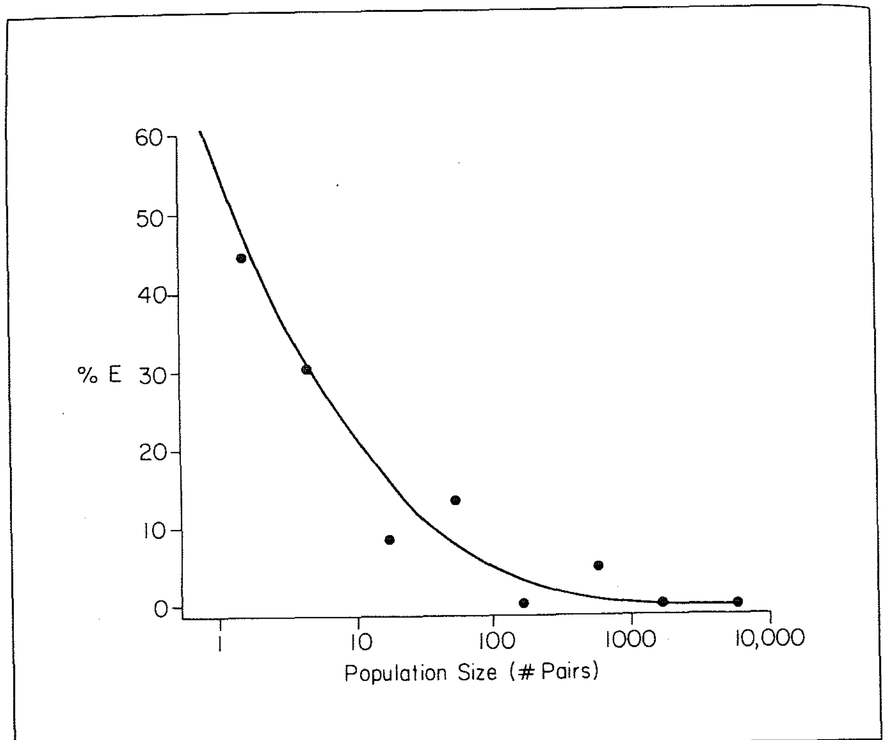

FIGURE 4. *Probability of extinction as a function of population size on the Channel Islands. On each island, the average breeding population of each species was estimated as falling into one of nine size classes (1 to 3 pairs, 4 to 10 pairs, 11 to 30 pairs,* etc.*). For each breeding population size class (abscissa), the ordinate gives as a percentage the number of populations in that class that became extinct since the first surveys, divided by the total number of populations in that class.*

extinction, independent of population size. For example, an island breeding population of Northern Ravens consisting of just two or three pairs can persist year after year, while equally small populations of a warbler would repeatedly go extinct and recolonize in the same length of time.

At this point, let us consider three common misconceptions that frequently arise in discussions of turnover.

(1) Some of the foregoing results could be misconstrued to mean that there are two types of populations: common species that breed regularly and do not turn over, and rare species that breed occasionally and do turn over. Is turnover only a constant churning of the rare species and a phenomenon of little importance to the bulk of the community? We do not believe that this is the case. Rather than there being two distinct types of species, there is, instead, a continuous decrease in risk of extinction with increasing population size (Fig. 4), and this rate of decrease differs for every species. A small population may last one year; a big one, 10 years; a still larger one, 50 years. A very large population becomes limited by its temporal coefficient of variation, rather than by population size itself, and may last a thousand or a million years. On a large island, many populations survive for a long time. That is why the oldest and most distinct endemic bird subspecies of the Channel Islands, the Island Scrub Jay, is on the largest island, Santa Cruz. On a small island, few populations survive for a long time. For example, on the smallest Channel Island, Anacapa, 24 species have bred at least once in this century, but, on the average, only 17 of these species breed in a given year, and only two of these species have populations currently exceeding 100 individuals; all the remaining populations on Anacapa are likely to have short lifetimes.

(2) So far, we have not said anything about the effects of man. One can ask if it is not true that much of this turnover is due to man and his fires, DDT, goats, sheep, and rabbits. To answer this question, we reviewed all the cases of turnover documented for the islands in relation to the history of habitat alteration, man's effect on the islands, and our experience with island birds and habitats (Jones and Diamond 1976). Some of the cases of turnover we observed are probably, or surely, due to the effects of man: the extinctions of Osprey, Peregrine Falcon, and Bald Eagle on all islands (see Kiff 1980); immigrations of European Starling and House Sparrow on some islands; and some extinctions due to habitat destruction, especially on Santa Barbara and San Clemente. However, the majority of the cases of turnover do not appear to be reasonably attributable to man. Instead, they seem to represent merely the fluctuations that one expects in any small population. For example, there is no obvious man-related reason why the Northern Mockingbird bred on San Nicolas in 1968, 1972, 1974, 1975, and 1976, but not in 1969, 1970, 1971, or 1973. As only one or two breeding pairs were involved, one could expect a large element of chance in determining whether a pair happens to breed in any particular year. The overall effect of man in this century may have been to decrease rather than to increase turnover rates by eliminating species that have rapid turnovers under natural conditions (*e.g.*, big raptors living at low densities) and by introducing species that have slow turnover rates (*e.g.*, the European Starling and House Sparrow).

This is partially, but not completely, offset by the long-term stability of raptor populations, despite their small size. Hunt and Hunt (1974) and Jones (1975) have shown, nevertheless, that carnivores on the Channel Islands have a higher turnover rate than do noncarnivores.

(3) The islands have endemic subspecies that may have taken a long time to evolve. Does this fact argue against several per cent of an island's species turning over every year? No, because different populations turn over at different rates. Some, like the Northern Mockingbird on San Nicolas, turn over almost every other year. Other populations, like some of the endemic subspecies, may last for tens of thousands of years. To illustrate species differences in turnover frequency, Figure 5 depicts the distribution of species among turnover frequency categories for two British islands. A turnover frequency of 0.5 would mean that a population immigrated or went extinct every other year, on the average. A turnover frequency of zero means that a population bred every year and never went extinct during the several decades for which censuses were available for these islands. This figure is based on the small island of Hilbre, which has only six breeding species in an average year, and on the larger island of Bardsey, with 26 breeding species in an average year. As the bar graphs illustrate, each island has some populations which turned over very rapidly (0.2 to 0.5/year, or once every several years), some populations which turned over slowly (0.1/year, once every ten years), and some populations which did not turn over at all within the span of censuses. There are many more populations with zero turnover frequency on the larger island than on the smaller island because almost all populations on Hilbre consist of too few breeding pairs to escape extinction for long.

Patterns similar to those shown in Figure 5 also apply to the Channel Islands and were

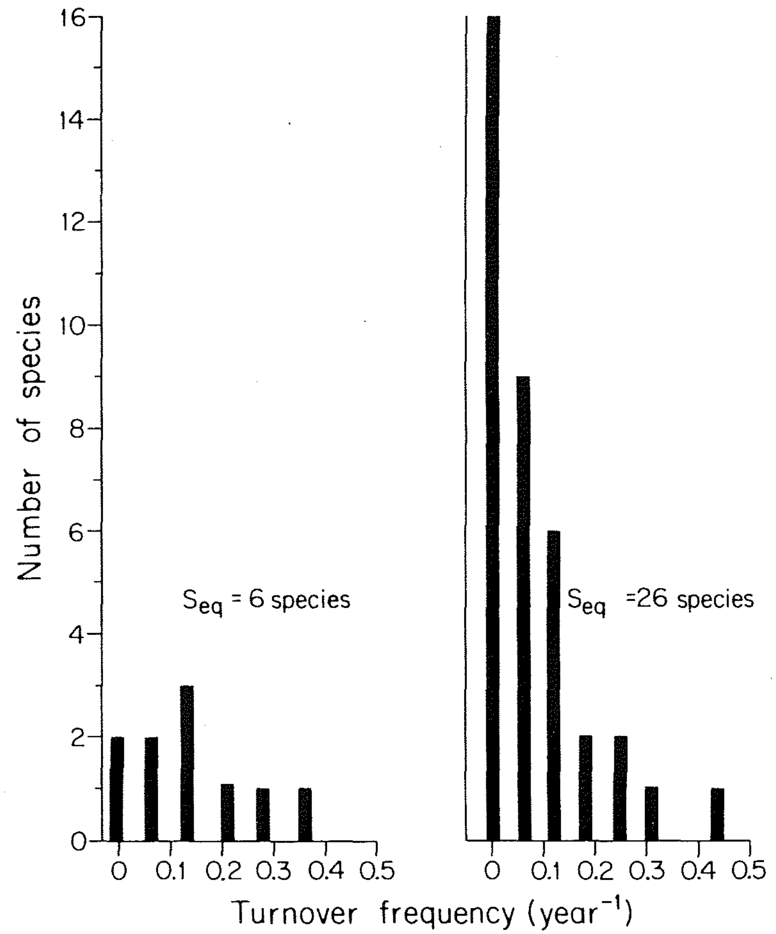

FIGURE 5. *Species differences in turnover frequency on the British islands of Hilbre (left) and Bardsey (right). Annual breeding surveys on each island for 16 or 17 consecutive years were analyzed. For each species that bred on the island during this period, the turnover frequency was calculated as the number of turnover events (immigrations or extinctions) over this 16- or 17-year period, divided by 16 or 17 years. Populations were then grouped according to turnover frequency; the bars indicate the number of species with a given turnover frequency. For example, a frequency of 0.2 year^{-1} means that a species exhibited three cases of turnover (immigration - extinction - immigration, or extinction - immigration - extinction) on the island in 15 years. On the average, the number of breeding species is six on Hilbre, 26 on Bardsey.*

illustrated previously (figs. 2 and 5 of Jones and Diamond 1976). For example, on San Nicolas, where the Northern Mockingbird turned over almost every year, the Horned Lark and House Finch have bred in every year of observation since at least 1897. On Santa Cruz, the Scrub Jay population has probably persisted for thousands or tens of thousands of years, while the Red-breasted Nuthatch has apparently immigrated and gone extinct repeatedly.

In the light of these observations, let us reconsider the favorite questions of island biogeographers: Why do islands have fewer species than the adjacent mainland? Why do small islands have fewer species than larger islands? Unfortunately, there is not just one simple answer. For Channel Islands birds, as for other species on other islands, there are at least three major explanations: (1) islands have fewer types of habitats than mainlands and small islands have fewer types of habitats than large islands; (2) some species never or rarely disperse over water to reach islands; and (3) local populations go extinct more often on islands than on the mainland, so that in a given year a smaller fraction of the island's species pool is present as breeders.

Other organisms may not necessarily show the same patterns as birds. Turnover rates must differ greatly among species groups, as pointed out by Wilcox (1980) in other contexts. Immigration rates are far lower for mammals, lizards, millipedes, and pine trees than for birds, butterflies, and annual weeds. For the former four groups of species, decades, centuries, or perhaps even millenia may elapse between immigration events. Extinctions may be much less frequent in small plants and insects than in birds, because there are many more individual plants and insects than birds per acre. Low extinction rates mean that a population may survive long enough to become an endemic species or subspecies. This may be why there are more striking endemics among Channel Islands plants and beetles than among birds: many plant and beetle populations, but few bird populations, have survived for a long time on the islands.

THE ENDEMIC BIRDS

While the islands have striking endemic species of plants and insects, there is no bird species confined to the Channel Islands. However, there are some endemic subspecies, as summarized by Johnson (1972). Of the 56 land bird species that breed or have bred on the islands, 13 are represented by one or more endemic races. In all, there are 18 currently recognized endemic races of birds on the Channel Islands, because some species are represented by two (Loggerhead Shrike) or three (Bewick's Wren, Song Sparrow) endemic races. The largest islands have the largest number of endemic populations.

The most distinctive endemic subspecies on the Channel Islands is the Scrub Jay population confined to Santa Cruz Island. Some other endemic races, such as those of the Orange-crowned Warbler and Horned Lark, are fairly distinct. Others are only weakly differentiated.

An interesting feature of the endemic avifauna is that two of the endemic subspecies, the island races of the Orange-crowned Warbler and Allen's Hummingbird, have established local breeding colonies on areas of the California mainland coast opposite the islands.

NICHE SHIFTS

The phenomenon of niche shifts is familiar from island studies elsewhere in the world and has contributed importantly to the rediscovery of interspecific competition in the past several decades (Diamond 1978). Briefly, island populations are often observed to occupy broader niches than populations of the same species on the mainland. For example, a species may occupy a wider range of habitats and occupy or forage over a broader altitudinal range on an island than on the mainland. The accepted interpretation of this phenomenon is based on the fact that there are fewer competing species on the islands. On the mainland, one species may be excluded by competing species from habitats and vertical zones in which its competitors are superior. On islands where these competitors are absent, the species is able to occupy these habitats and zones. Yeaton (1974) has published a detailed analysis of niche shifts on Santa Cruz Island, and Diamond (1970) has described other examples.

Compare, for example, the breeding bird communities in chaparral on Santa Cruz or other Channel Islands and on the mainland. The total number of breeding bird pairs per acre of chaparral is similar on Santa Cruz and on the mainland. Yet Santa Cruz chaparral has only two-thirds as many breeding species as mainland chaparral has, and some of the commonest species found in mainland chaparral are completely absent on Santa Cruz: the Wrentit, Brown Towhee, California Thrasher, Plain Titmouse, and Nuttall's Woodpecker. Other Channel Islands are even more impoverished, lacking the Scrub Jay and Bushtit of Santa Cruz Island and mainland chaparral. What makes up for the missing species on Santa Cruz? Which Santa Cruz birds utilize the extra resources made available by the absence of mainland competitors?

In part, the resources are used by species that also occur in mainland chaparral but are more abundant in Santa Cruz chaparral. For example, Bewick's Wren is twice as common and Hutton's Vireo four times as common in Santa Cruz chaparral as in mainland chaparral.

The resources are also used by species that are confined to habitats other than chaparral on the mainland. Excluded from mainland chaparral by competitors, they are able to move into Santa Cruz chaparral because of the absence of these competitors.

For example, on the mainland, Allen's Hummingbird breeds in the coastal zone and is largely excluded from chaparral by Anna's Hummingbird. On the islands, Anna's Hummingbird is uncommon or absent, while Allen's Hummingbird is common in chaparral.

On the mainland, the Scrub Jay occupies chaparral and oak woodland communities. On Santa Cruz Island, it can also be found in Bishop Pines, which lack the similar Steller's Jay of Bishop Pine communities on the mainland.

The common insectivores of mainland chaparral are the Wrentit, Bushtit, and Plain Titmouse. They are replaced in island chaparral by the Orange-crowned Warbler, which is uncommon or absent in mainland chaparral, and by a superabundance of the Bewick's Wren, Hutton's Vireo, and Blue-gray Gnatcatcher, compared with the numbers found in mainland chaparral.

The common mimic thrush of mainland chaparral is the California Thrasher. On Santa Cruz, it may be replaced partly by the Northern Mockingbird, which is uncommon or absent in mainland chaparral, and, perhaps, partly by the island race of Scrub Jay, which has been described as spending much time feeding on the ground, as the California Thrasher does on the mainland.

These are some of the examples of niche shifts that become apparent if one compares communities in the same habitat on an island and on the mainland, or on different islands. All these niche shifts illustrate the same point: those species that reach islands successfully may increase their abundance or broaden their niches by utilizing resources that would have been pre-empted by mainland competitors.

SUMMARY

Fifty-six species of land birds are known to breed, or to have bred, on the eight California Channel Islands. Based on information in the literature and on our own field surveys conducted in 1968 and from 1973 through 1977, we categorize these species according to breeding status and to whether or not they have recently immigrated and established breeding populations or have formerly bred and become extinct. Populations on the islands are not static but are in a dynamic equilibrium (*i.e.*, species composition varies through time). Average annual turnover of island populations is one to six per cent per year. True turnover rates must be based on one-year census intervals. Data from the Channel Islands and certain European islands exhibit a drastic decline in *apparent* turnover rate with increasing census interval; census intervals of a decade or more underestimate the turnover rate by about an order of magnitude.

There is a continuous decrease in risk of extinction with increasing population size. Smaller, more extinction-prone populations are commonly those species with large territories (*e.g.*, large raptors), species in specialized habitats, and species on small islands. Different populations turn over at very different rates. Furthermore, the majority of cases of turnover do not appear to be attributable to the effects of man.

Turnover rates are higher and the degree of endemism is lower for more mobile species, such as birds, than for less mobile organisms, such as most mammals, reptiles, amphibians, and plants. There are a number of cases of increased densities and niche shifts for island birds. Those species that succeed in reaching islands may increase their abundance or broaden their niches by using resources that would have been pre-empted by competitors on the mainland.

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Evolution of Land Birds on the California Islands

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INTRODUCTION

Knowledge of island plants and animals can contribute significantly to our understanding of speciation. On oceanic islands, isolation and new selective forces often lead to dramatic evolution. Adaptive radiation in Galapagos finches, for example, has become well known (Darwin 1845, Lack 1945, Bowman 1961). On near-shore, continental islands, genetic changes in populations are commonly not as great, being usually at the species level in sedentary forms and at the subspecies level in more mobile ones. This can be due to gene flow and to the fact that the physical and biotic differences, compared with those on the mainland, are usually less for fringing islands than for oceanic ones.

On an assemblage of oceanic islands, divergent populations on different islands may show similarities to each other, but their mainland ancestor may not be readily identifiable. With continental islands, a mainland form (usually an ancestor) often is identifiable and can be compared with the island populations (usually derived species or races). In such comparisons some interesting trends have been discovered. For example, Murphy (1938) found that 21 of 27 North American passerine birds breeding on islands have, on the average, larger bills than their nearest mainland relative. Grant (1965a, 1965b), summarizing size trends in island birds of North America, and in particular those of the Tres Marías Islands, Mexico, found that there is a strong tendency for island passerines to have a longer tarsus and bill than their mainland counterparts. However, island forms do not tend to have longer wings and tail. Grant believes that a longer bill is correlated with a greater range of food sizes and that the tarsus is longer because a greater variety of perches is used. He argued that these differences have arisen as a result of an absence or a reduction in the number of competing species, allowing those forms that are present to occupy wider niches and, in some cases, totally new habitats. In another case, Foster (1963) reported on the relative sizes of 12 species of land birds on the Queen Charlotte Islands, British Columbia. On the average, in most island populations the tarsus was larger; bills were longer in many island populations, as well. Wing and tail measurements did not tend to differ from mainland conspecifics in Foster's study.

The first noteworthy comparative analysis of birds on the California Island was by Ridgway (1877) and concerned only Guadalupe Island (Fig. 1). Ridgway (1877:60) wrote:

> The more prominent characteristics of these Guadalupe birds, as compared with the mainland forms, are (1) increased size of the bill and feet, (2) shorter wings and tail, and (3) darker colors; these variations are by no means uniform, however, in the several species, the differentiation being in some slight, while in others it amounts to almost generic distinctness.

More recently, Johnson (1972:313) wrote on the origin and differentiation of the avifauna of the Southern California Channel Islands, and stated:

> Of the approximately 41 species of land birds which breed on 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