

SHORT-TIME-BASE STUDIES OF TURNOVER IN BREEDING BIRD POPULATIONS ON THE CALIFORNIA CHANNEL ISLANDS

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The number and identities of species coexisting at a particular locality are not fixed forever, but result from dynamic interplay between local extinctions and immigrations. While this dynamic structure must apply to any local community, it is particularly convenient to study on islands, because of their sharp boundaries. In their well-known theory of island biogeography MacArthur and Wilson (1963, 1967) proposed that the number of species on an island approaches an equilibrium between extinctions and immigrations, and that populations are subject to turnover. It is likely that large differences in turnover rates will be found if one compares the same taxonomic groups on islands of different area, isolation, latitude, and habitat, or if one compares different species on the same island. The measurement and understanding of these differences is beginning to emerge as a major empirical and theoretical problem in ecology (Maguire 1963, Patrick 1967, Simberloff and Wilson 1969, Diamond 1969, 1971, Terborgh and Faaborg 1973, Hunt and Hunt 1974, Schoener 1974), as a problem in assessing the importance of group selection and understanding the evolution of social behavior (Levins 1975, Wilson 1975:115-116), and as a major practical problem in conservation strategy (Terborgh 1974a, 1974b, Diamond 1975, 1976, Wilson and Willis 1975, Sullivan and Shaffer 1975).

A convenient situation for studying these problems is provided by the land and freshwater breeding birds of the Channel Islands off the coast of southern California. The eight islands of this group vary in area (A) from 2.6 to 249 km², in distance from the mainland (d) from 20 to 98 km, and in number of land and non-swimming water bird species breeding in a given year (S_{eq}) from 7 to 39 (see Philbrick 1967, Power 1972, Johnson 1972, and Jones 1975 for maps and table of areas and distances). As of 1917, when A. B. Howell's monograph *Avifauna of the Islands off the Coast of Southern California* was published, 170 species of birds had been recorded from the Channel Islands. By 1976 this number had increased to 325. All but five of these 155

additions were of non-breeding visitors, recorded principally by us and by other observers since 1968. The reason is that most of the early ornithologists who visited these islands were collectors and oologists mainly interested in obtaining specimens or egg sets of the breeding birds, some of which are considered endemic or nearly endemic subspecies. Consequently, the breeding avifauna of all the Channel Islands was more thoroughly documented by 1917 than was the non-breeding avifauna (see appendix p. 545 for discussion).

In 1968 one of us (J. D.) visited each of the Channel Islands 1-3 times, plus the nearby Mexican island group Los Coronados, to survey the breeding avifaunas for comparison with the surveys summarized by Howell (1917). On each island he found that there had been turnover, reflected both in disappearances of some former breeding populations and in breeding presence of some formerly absent or non-breeding species. A brief account of the results, and of estimated turnover rates in relation to A , d , and S_{eq} , was published (Diamond 1969). One of Diamond's findings was that some breeding populations had immigrated and become extinct several times on the same island between the early 1900's and 1968. Thus, surveys separated by many decades must have underestimated turnover rates and might only have revealed the tip of the iceberg of community dynamics (see Diamond and May in press for examples). For organisms as mobile as birds, and islands as close to the mainland as the Channel Islands, it is likely that there will always be a long waiting list of potential immigrants; many more unsuccessful attempts at colonization than attempts that succeed even briefly; and many more brief successes and rapid failures than foundings of a colonist population that survives a long time. Hence repeated surveys at one-year intervals were clearly required to reveal the dynamic structure of the avifauna more accurately. Such studies of turnover at one-year intervals have the further advantage of reducing interpretative problems associated with habitat changes and effects of man which develop over longer intervals.

In 1973, L. J. began a program of annual breeding surveys of all eight Channel Islands. This program is now entering its fifth year. Surveys of some of the islands by other observers for certain years between 1969 and 1972 are also available. The purpose of this paper is four-fold: to report the problems encountered and methods used in these short-time-base turnover studies; to illustrate and describe the rich spectrum of dynamic behavior they reveal; to discuss the several ways in which man has directly and indirectly increased and decreased turnover rates; and to present estimated turnover rates, evidence for dynamic equilibrium of species number, and a model of island colonization. Species accounts of the Channel Islands avifauna, with details of records and with descriptions of island habitats and history, are being prepared for publication in book form elsewhere (Jones 1975 and in prep.). An appendix considers critiques of turnover studies by Johnson (1972) and by Lynch and Johnson (1973, 1974).

METHODS

SOURCES OF INFORMATION

The present paper is based on island visits by L. J. from February 1973 through August 1976. During this period, which included four breeding seasons, he visited the islands 150 times for periods of up to 15 days per visit and accumulated approximately 2699 hours of field observation (table 1, columns 5 and 6). The number of accumulated visits by Jones to any one island ranges from 10 (San Miguel) to 34 (San Nicolas); of accumulated hours of field observation on one island, from 172 (Anacapa) to 1008 (San Nicolas). Visits were made in all months of the year. Most visits were in the breeding season, but some were made outside the breeding season to assess resident status of populations. Additional observers accompanied Jones on many of these visits.

During the 1968-1976 period many other biologists contributed additional surveys or records, of which the most extensive are the following. In the 1968 breeding season teams of biologists from the Smithsonian Institution's Pacific Ocean Biological Survey Project visited six of the eight islands up to three times each, and maintained a resident observer on San Nicolas for most of the breeding season. G. and M. Hunt lived on Santa Barbara for most of the breeding season from 1972 to 1976; R. Yeaton on Santa Cruz in 1969 and 1970; D. Propst on Santa Catalina from 1968 (and earlier) through 1976; L. Laughrin on Santa Cruz from 1969 through 1976; D. Lees on Santa Catalina in 1968; and R. DeLong on San Miguel in 1972 and 1973. D. Odell made numerous visits to Santa Barbara in 1968 and to San Nicolas from 1969 to 1971, and lived on San Nicolas for part of this time. J. Larson and associates from the Naval Underseas Center and California State University at San Diego made numerous visits to San Clemente from 1972 to 1976; F. Gress, 13 visits to Anacapa in 1970; R. Stewart and W. Clow, two visits to San Clemente in 1974.

TABLE 1. Ornithological visits to the Channel Islands.

Island	Earlier observers			Jones	
	first year	visits	years	visits	field hours
San Miguel	1875	30	24	10	241
Santa Rosa	1889	22	16	13	220
Santa Cruz	1875	103	47	14	274
Anacapa	1899	60	35	27	172
San Nicolas	1863	24	17	34	1008
Santa Barbara	1863	32	25	25	317
Santa Catalina	1861	70	43	16	215
San Clemente	1863	46	33	11	252
				150	2699

For each island the table gives the year of the first ornithological observations; the approximate number of visits by ornithologists, and number of years in which there were visits, through 1967; and the number of visits and accumulated field hours by Jones. The number of visits since 1967 by observers other than Jones is too large to tally.

J. Atwood visited Santa Cruz a number of times in 1975 and 1976. As part of our survey program, K. Garrett made four visits to Anacapa, two to Santa Barbara, and one to San Clemente in 1975 and three to Anacapa in 1976; G. and S. Grant, three visits to Santa Catalina in 1975 and one in 1976; D. and G. Schroeder, one visit each to San Miguel, Santa Rosa, Santa Catalina and San Clemente in 1976 and six visits to Santa Cruz; P. Unitt, one visit each to San Clemente and San Miguel in 1976; R. Higson, one visit to Santa Cruz and Santa Catalina in 1976. Many other individuals contributed additional observations.

In addition, we critically evaluated all published papers known to us that discuss Channel Island birds, from 1868 to the present. Numerous unpublished manuscripts and field notes of ornithologists who visited the Channel Islands were found, especially in the libraries and Dickey Collection at UCLA, at the Museum of Vertebrate Zoology (Berkeley), and at the Western Foundation of Vertebrate Zoology (Los Angeles), and were similarly critically evaluated. Significant unpublished manuscripts dating back to at least 1927 were found for all islands, and back to 1897 for some islands. Published and unpublished general accounts of the Channel Islands, not dealing specifically with birds, were studied in order to reconstruct the history of habitat changes and human disturbance; such information was available for all islands at least from the 1840's. Jones examined the collections of egg sets and bird specimens from the Channel Islands in the following museums and universities: California Academy of Sciences Museum (including Stanford University collections), Santa Barbara Museum of Natural History, Los Angeles County Museum of Natural History, Western Foundation of Vertebrate Zoology (WVZ), San Bernardino County Museum, San Diego Natural History Museum, Museum of Vertebrate Zoology (MVZ), UCLA Dickey Collection, and California State University at Long Beach. Some of the specimens and unpublished manuscripts that we examined for years prior to 1917 were evidently not available to Howell (1917) when he prepared his review of the avifauna. Conclusions about breeding status reached by Diamond (1969) have been reassessed in the light of additional information encountered for years prior to 1968 and of our observations since 1968. Because details of records will be published elsewhere (Jones, in prep.) and

would increase the length of this paper prohibitively, we cite references only for some key records obtained before our observations began in 1968.

The years for which it proved possible to compile reasonably complete lists of breeding birds to use for turnover calculations (p. 539) are as follows for each island: San Nicolas 1897, 1945, 1962–1963, 1968, 1973, 1974, 1975, 1976; Santa Barbara 1897, 1911–1912, 1968, 1972, 1973, 1974, 1975, 1976; Anacapa 1910–1912, 1939–1941, 1963–1964, 1968, 1970, 1973, 1974, 1975, 1976; San Miguel 1939, 1968, 1973, 1975, 1976; San Clemente 1897, 1907, 1915, 1968, 1973, 1974, 1975, 1976; Santa Catalina 1905–1909, 1968, 1973–1974, 1975, 1976; Santa Rosa, 1927, 1968, 1973, 1974, 1976; Santa Cruz 1911–1912, 1968, 1973–1974, 1975, 1976. In the nine cases of years connected by a hyphen, we based such breeding lists on observations made over several consecutive years (p. 545). Table 1 lists, for each island, the number of ornithological visits through 1967 which we were able to locate as sources of bird records, based on published papers, museum specimen data, or unpublished manuscripts or field notes; the year of the first visit by an ornithologist; and the number of years through 1967 in which at least one visit was made, as well as details of Jones's visits. Since results of the great majority of visits to the Channel Islands have remained unpublished, a search of only the published literature would grossly underestimate the amount of field work that has been done.

SURVEY STRATEGY

Field time on the islands was allocated with two primary purposes in mind: to determine which of the species observed on a particular island were breeding and which were not, in most cases by locating active nests and fledglings, in some cases (see next section) by observing other indications of breeding; and to minimize the likelihood of overlooking species that might be breeding. Whenever a visit yielded inconclusive evidence of breeding for a particular species, we attempted to return or to have a resident observer return to the same site later to resolve the question.

Regarding the problem of breeding populations being overlooked, two islands, Santa Barbara and Anacapa, are sufficiently small (2.6 and 2.9 km², respectively) that it was feasible to examine essentially the whole island. On the five largest islands (Santa Cruz, Santa Catalina, Santa Rosa, San Clemente, San Nicolas) the availability of roads, jeep transportation, and resident observers facilitated surveys. On these five islands plus the medium-sized San Miguel (36 km²) we used our experience of island habitats and recent breeding populations to design survey strategies. Particular attention was paid to specialized habitats or to species-rich habitats likely to harbor local populations, such as springs, wind-sheltered gullies, streams, marshes, wooded canyons, and pine forest. Some field time was allocated at night to find nocturnal species. A measure of the completeness that it proved possible to attain is that although much additional information was available from other observers for each island in each survey year as discussed in the preceding section, both Diamond in 1968 and Jones in 1973–5 themselves observed almost all breeding populations each year except for some owl populations on the four largest islands, reliably reported to us by other observers. We have not attempted to assess turnover in these large-island owl populations. In practice, it has become clear that turnover rates are much the highest on the smallest

islands (p. 540), which have the advantage of being the easiest islands to survey completely and on which to prove turnover. The possibility remains for the larger islands that we overlooked one or more species of which only one or two pairs bred in single years. We have no reason to suspect having overlooked such cases, but if we did, actual turnover rates for larger islands would be higher than those we report. For purposes of calculating immigration and extinction rates in the Channel Islands avifaunas, we have considered only the breeding avifauna, defined as those species of which at least one pair is known, or may reasonably be inferred, to have attempted to nest on the particular island in the year considered, regardless of whether or not the nest attempt finally resulted in fledged young. Only bird species that do not normally rest on salt water were considered (i.e., gulls, ducks, and alcids were excluded; shorebirds, waders, and Rallidae were included).

The Channel Islands are visited by many non-breeding migrants and vagrants. Many migrant passerines sing and even behave territorially for short periods. Therefore, one of the main practical problems to which our field observations were devoted was to establish which species were breeding on each island. In most cases that we accept as instances of turnover, proof was obtained by observing active nests or fledglings, and the existence of such evidence is implied in all instances in the text when we discuss turnover without otherwise citing breeding evidence. However, in a minority of cases one or more pair of a species were found to be resident on an island during the breeding season at a constant location in appropriate breeding habitat, and other types of evidence indicated breeding, but the nest or fledglings could not be seen. To ignore such cases would introduce probable errors into turnover calculations. In such cases, availability of one or more of the following types of evidence, cited in the text by the code letter in parentheses, was accepted in conjunction with residency as evidence of breeding: (m)—Adults were repeatedly seen carrying nest construction material to a place or carrying egg shells or fecal sacs from a place. (f)—Adults were repeatedly seen carrying food to a presumed nest. (s)—Adults of hole-nesting or cliff-nesting species were repeatedly seen entering a presumed nest site in a hole or on a cliff inaccessible to us for direct observation. These cases involved Acorn Woodpecker (*Melanerpes formicivorus*) and American Kestrel (*Falco sparverius*). (j)—Juveniles were observed that were capable of flight but had incomplete feather growth, were accompanied by adults and often were being fed by the adults, and were presumed to have been fledged recently on the island of observation. (t)—One or more pair of adults exhibited clear territorial behavior for a prolonged period in the breeding season. Whether such behavior provides any evidence at all of breeding depends entirely on the species, number of pairs involved, and length of time involved, as discussed for each case in the text (e.g., see discussion of Hutton's Vireo (*Vireo huttoni*) on p. 535).

Questions of breeding status were evaluated conservatively with respect to turnover calculations if evidence was inconclusive. That is, if a species was represented on an island in the breeding season, but if available evidence did not suffice to make breeding either highly likely or highly unlikely, the species was assumed to be breeding if this was true in previous and subsequent survey years, and was assumed to be not

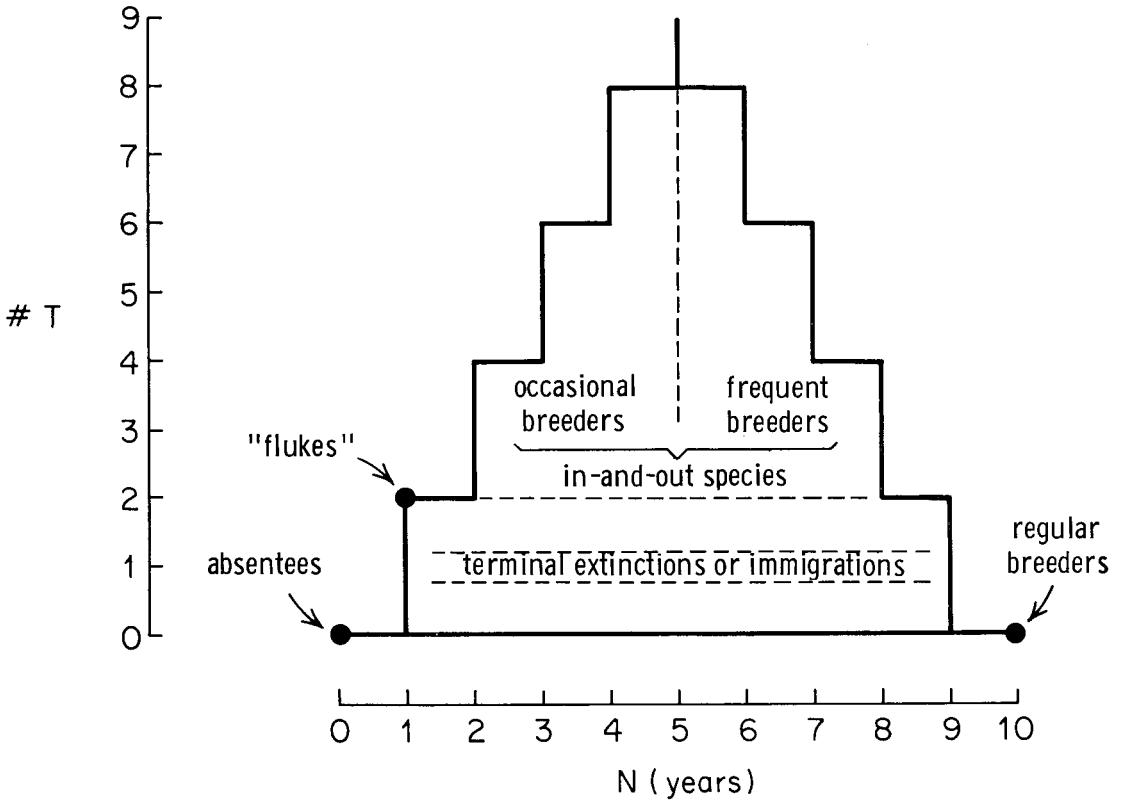


FIGURE 1. Turnover pyramid. Abscissa: number of years, out of 10 survey years, that a particular species bred on a particular island (e.g., $N = 10$ means that the species bred every year). Ordinate: number of cases of turnover, counting either an immigration or an extinction as one case of turnover, that the species provided on the island within the 10 survey years.

breeding if this was the case in previous and subsequent survey years. If a year of definite breeding was separated from a year of definite absence by a year of presence with uncertain breeding status, the decision affects the calculated time of turnover but not the calculated number of cases of turnover. In such cases we arbitrarily assumed the immigration to precede and the extinction to follow the uncertain year. Barn Owl (*Tyto alba*), Saw-whet Owl (*Aegolius acadicus*), and Burrowing Owl (*Athene cucularia*) are sufficiently difficult to observe, to prove absent, or to document as nesting that we conservatively assumed no case of turnover for Barn or Saw-whet owl and only two particularly well documented cases for Burrowing Owl. In evaluating surveys by earlier observers before our field work began, we considered lack of records for a particular species in a particular year as evidence of actual absence only if the intensity of the survey in relation to the size of the island and ease of observation of the species made the lack of records significant. For instance, the failure of Joseph Grinnell to find the conspicuous Peregrine Falcon (*Falco peregrinus*) on a six-day visit to tiny Santa Barbara in 1897 is considered sufficient evidence for absence that we count a subsequent breeding record as an immigration. However, the failure of Green, Sumner, and Bond to find the Barn Owl on San Miguel during two visits in 1938 and 1939 is not considered sufficiently strong evidence of absence to warrant counting a nest found in 1968 as proof of an immigration of this nocturnal species.

RESULTS

THE TURNOVER PYRAMID

Suppose that complete breeding censuses of an island were available for, say, 10 separate years. The results for each species might be depicted in short-hand by numbering the years, underlining years of breeding, and denoting immigrations by I and extinctions by E: e.g., 1E2I3E4I5E6I7E8I9E10, or 1234E567-I8910. The turnover characteristics of each species could then be depicted by plotting the species as a point in a two-dimensional space, as illustrated in figure 1. The horizontal axis of this space is the number of years (N) out of the 10 survey years that the species bred. The vertical axis is the number of cases of turnover ($\#T$) which that species provided, counting either an immigration or an extinction as one case of turnover. Points for all species are constrained to be within a pyramid whose apex is at $N = 5$, $\#T = 9$ (corresponding, e.g., to 1E2I3E4I5E6I7E8I9E10). To understand the step-walled form of the pyramid, consider that $N = 2$ years can correspond to

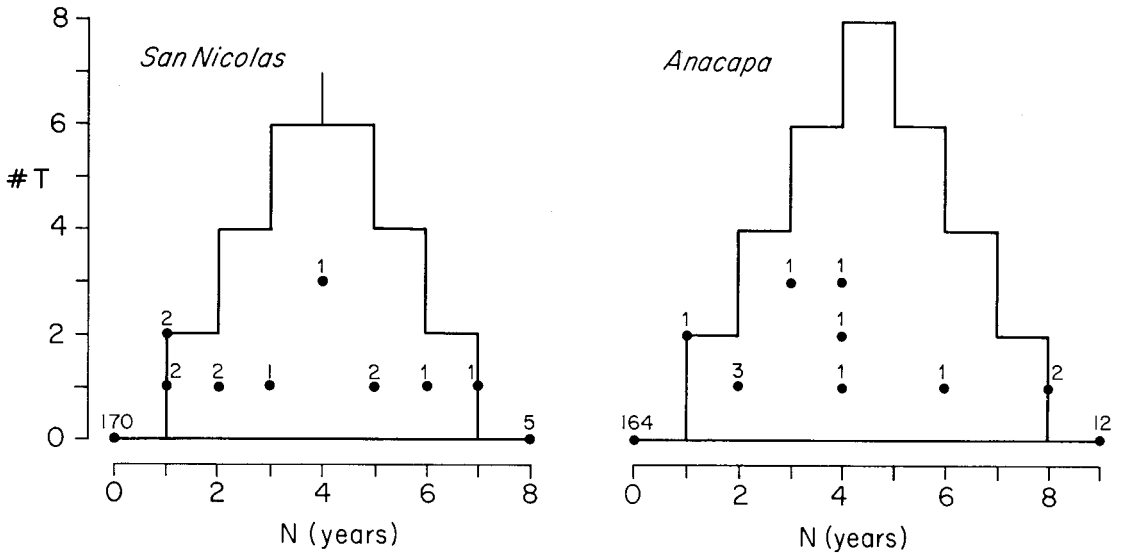


FIGURE 2. Turnover pyramids for San Nicolas and Anacapa islands, based on the survey years listed in the text. Numbers above the points are the number of species with the indicated ($\#T, N$) value. The value for the number of absentees ($\#T = 0 = N$) was obtained by subtracting the number of species that have bred on San Nicolas or Anacapa from the 187 species that breed on the southern California mainland.

$\#T = 1$ case (e.g., 12E345678910), 2 cases (e.g., 1123E45678910), 3 cases (e.g., 1E2345-16E78910) or 4 cases (e.g., 1213E4516E78910), but not $\#T = 0$ or ≥ 5 cases.

Points can be anywhere corresponding to integral values of N and $\#T$ within the pyramid, so that species can form a virtual continuum in their turnover characteristics. However, it is convenient arbitrarily to divide and name different parts of the pyramid's space as corresponding to different "types" of populations. Points at $N = 10, \#T = 0$ correspond to "regular breeders" that never turn over within the survey period. Points at $N = 0, \#T = 0$ also correspond to species that never turn over, but because they never breed ("absentees"). Points at $\#T = 1$ represent either "terminal extinctions" (species that breed in the first years censused, disappear, and do not return) or else "terminal immigrations" (species that are absent in the first years censused, colonize, and remain). Points at $N = 1, \#T = 2$ represent "flukes": improbable colonists that manage to breed one year but immediately disappear. The remaining points ($\#T \geq 2, N \geq 2$) constitute "in-and-out species" that frequently immigrate and become extinct again, and that may be further designated either as occasional breeders ($N \leq 5$) or frequent breeders ($N \geq 5$).

Figure 2 gives two examples of actual turnover pyramids, based on Anacapa and on San Nicolas. Of the 23 species that bred on Ana-

capa in one or more of nine survey years, 11 were established as having participated in turnover. Two species turned over three times each, two turned over twice each, and seven others turned over once each. Of the 17 species that bred on San Nicolas in one or more of eight survey years, one species turned over three times, two turned over twice, and nine more turned over once each. Of the remaining 17 species on these two islands, for which turnover was not proved, some may nevertheless have participated in undetected turnover, since proof of nesting in all years was not obtained for most species. However, since evidence of breeding absence is also not compelling for these remaining species in any year, we have conservatively assumed no turnover for them, and figure 2 gives minimum estimates of turnover.

We present turnover findings for the Channel Islands by assigning all populations ever known to have bred to one of several categories discussed below, proceeding from zero-turnover populations to flukes. Since the categories intergrade, assignments to categories are of course somewhat arbitrary. Populations of one species may belong to different categories on different islands. For example, the Red-tailed Hawk (*Buteo jamaicensis*) is a regular breeder on Santa Cruz, Santa Catalina, and Santa Rosa, absent on San Nicolas and Santa Barbara, a terminal immigrant on San Miguel, and an in-and-out species on San Clemente and Anacapa.

ZERO TURNOVER: REGULAR BREEDERS

Jones (1975, in prep.) summarized the populations that are known or assumed to have bred in each survey year, and for which there is no evidence of turnover. Only 12 of the 56 species known to have bred on the Channel Islands are not known to have participated in turnover. Some regularly breeding populations have undergone large fluctuations in breeding abundance that have at times brought them close to extinction. For example, on Anacapa, the House Finch (*Carpodacus mexicanus*) was one of the three commonest species in 1910 (Willett 1910), was considered not particularly common by 1963 and 1964 (Banks 1966), had declined to about six individuals by the 1968 breeding season (J. D.'s observations), and recovered to about 15 individuals in 1973, 30 in 1974, and 20–30 in 1975 and 1976 (L. J.'s observations). On the large island of Santa Rosa, the Northern Mockingbird (*Mimus polyglottos*) was "common" in 1927 (Pemberton 1928), was widespread and numbered about 400 individuals in 1968, but had declined to about 30 sparsely distributed individuals by 1973. Conversely, the Orange-crowned Warbler (*Vermivora celata*) on Santa Rosa was common in 1927, had become confined to Lobo Canyon and numbered only about 20 individuals in the 1968 breeding season, but had again become ubiquitous in all wooded canyons and in chaparral and coastal sage scrub by the 1973 breeding season, when the estimated population was 1200. Thus, even populations with a high time-averaged abundance on large islands occasionally crash to dangerously low levels. In the long run, it will be the frequency and magnitude of these crashes (the temporal coefficient of variation), as shown by Leigh (1975), rather than the time-averaged abundance, that determines the extinction probability of these large populations.

ZERO TURNOVER: ABSENTEES

Species that have never bred on some or all islands can be subdivided into at least five categories. First, some species that breed on the southern California mainland in habitats represented on the islands have never been recorded from the Channel Islands, even as vagrant individuals. Some of these species are such weak fliers that they may be physically incapable of reaching even the nearest island (Anacapa, 20 km from the mainland). Such species may include the Greater Roadrunner (*Geococcyx californianus*), Wrentit (*Chamaea fasciata*), and California Thrasher (*Tox-*

ostoma redivivum). Other species not recorded from the islands are strong fliers such as the Red-shouldered Hawk (*Buteo lineatus*) or average fliers such as the Downy Woodpecker (*Picoides pubescens*), Nuttall's Woodpecker (*P. nuttallii*), Common Screech Owl (*Otus asio*), Plain Titmouse (*Parus inornatus*), and Brown Towhee (*Pipilo fuscus*). Mainland populations of all these species are, nevertheless, very sedentary. Still other species are strong fliers and long-distance migrants overland but, nevertheless, have not been recorded on the Channel Islands. The Black-chinned Hummingbird (*Archilochus alexandri*), for example, migrates to central Mexico from coastal southern California, yet has never been recorded from the Channel Islands.

In a second category are species that do reach islands with suitable habitat but arrive so rarely or in such low numbers that the chances of establishing a breeding pair are low and breeding success has not materialized to date. For example, in 1927, around the time that Acorn Woodpeckers invaded and established themselves on Santa Cruz, two individuals were seen on Santa Rosa (Pemberton 1928), which offers considerable areas of suitable habitat. None has been seen there since, so that these few individuals must soon have disappeared, although an invasion of more colonists might have succeeded. From February 1974 to late April or May 1975 a single Red-tailed Hawk was resident on San Nicolas, but a second individual did not arrive. Because this hawk breeds on San Miguel, which has similar habitat and a smaller area, breeding might well have taken place on San Nicolas had a mate arrived. Since August 1973 a single Cañon Wren (*Catherpes mexicanus*) has been resident on Santa Cruz in a habitat typical of this species. To date, a mate for this individual has not arrived. Acorn Woodpeckers, Cañon Wrens, and Red-tailed Hawks all differ from the first category of absentees in that they do occasionally reach islands, but their colonizations are infrequent.

A third category of absentees consists of species that reach islands but find no suitable breeding habitat. In this category are the dozens of Sierran and northern species that flood all the islands every year on spring or fall migration or in the winter but breed on no island. Other examples are numerous vagile species that reach all islands each year and breed only on those islands that offer suitable habitat (e.g., Common Flicker, *Colaptes aera-*

tus, and Western Flycatcher, *Empidonax dif-
ficilis*).

The fourth category of absentees includes species which often reach islands with suitable habitat but whose failure to breed is probably due to the presence of established, abundant competitors. For example, the widespread abundance of Allen's Hummingbird (*Selasphorus sasin*) may explain the failure of Anna's Hummingbird (*Calypte anna*) and Costa's Hummingbird (*C. costae*) to establish lasting breeding populations on most islands. Likewise, among the four species of sparrows that breed on the islands, the breeding absence of some species on islands where they might be expected may be due to the established breeding presence of other species.

The last category of absentees consists of long-distance migrants that winter south of the United States, breed in habitats on the southern California mainland also represented on the islands, apparently lack close competitors on the islands, and flood the islands during spring migration each year, but nevertheless fail to breed. These species present one of the most puzzling problems in the island avifauna. Examples are the Ash-throated Flycatcher (*Myiarchus cinerascens*) and Black-headed Grosbeak (*Pheucticus melanocephalus*), for which the arborescent chaparral and woodland of Santa Catalina, Santa Cruz, and Santa Rosa provide typical breeding habitat; the Warbling Vireo (*Vireo gilvus*) and Northern Oriole (*Icterus galbula*), for which riparian woodland on the same three islands seems equally suitable; and the Cliff Swallow (*Petrochelidon pyrrhonota*). While one can never refute the ad hoc interpretation that the islands lack some subtle ecological factor important to these species but invisible to ornithologists, the island habitats seem to us and to others with whom we have discussed these species well within the broad range of habitats occupied on the mainland. In addition, the Ash-throated Flycatcher and the Black-headed Grosbeak refuted this interpretation by starting in the 1960's to breed annually in small numbers and in the expected habitat on Santa Cruz (p. 533), although they had already previously been recorded as spring migrants on Santa Cruz and are still migrating annually through similar habitats on Santa Catalina and Santa Rosa without breeding. We can only guess that these are strongly philopatric species which return annually to the same breeding area despite great distances between breeding and wintering sites. The establishment of the flycatcher and grosbeak

on Santa Cruz may initially have involved only a single pair, whose offspring returned. Two examples support this interpretation. First, the island population of Western Flycatchers is considered an endemic subspecies, of which all individuals leave each fall to winter in Central America and return the following spring. Second, banding studies on the mainland have shown that Cliff Swallows do return year after year to the same nest site, whereas Barn Swallows (*Hirundo rustica*), which have successfully colonized all eight islands, are much less philopatric (Speich, pers. comm.).

TERMINAL IMMIGRATIONS

The following populations became established on islands, have continued to breed, apparently without interruption, and are sufficiently numerous that they are likely to survive some time longer.

The sole island on which American Kestrels had been proven to breed in the early decades of this century was Santa Cruz (nest records in 1906 and 1919). Evidence that they actually did not breed is adequate for at least five islands. Early visits to Santa Barbara (in 13 years between 1863 and 1918) and Santa Catalina (in 21 years between 1861 and 1919) failed to record this conspicuous species at all. It was recorded on San Clemente in 1907 but not in 15 other years between 1863 and 1920. San Miguel yielded only one specimen taken at an unspecified date in 1910 and no observations during visits in 1927, 1938, and 1939. On San Nicolas it was recorded only as a winter visitor prior to 1975 and did not breed until 1976. The early status on Anacapa and Santa Rosa is uncertain, because there was a single March record for the former in 1911 without proof of breeding, and because ornithological exploration of the latter before the first kestrel record in 1927 was incomplete. At present the American Kestrel is breeding on all islands, with nests found on five islands and type-s, -t, and -j evidence (see p. 528) available for three islands.

American Coots (*Fulica americana*) first appeared on Santa Catalina in the winters of 1928 and 1929 (Meadows 1929) following construction of a man-made freshwater reservoir, where coots have bred annually since at least 1967.

There have been 2-5 American Oystercatchers (*Haematopus palliatus*) on Santa Cruz since at least 1966, where they are apparently interbreeding freely with Black Oystercatchers (*H. bachmani*).

Except for one winter record on Santa Cruz in 1907, there were no observations of Killdeers (*Charadrius vociferus*) on any island until 1927 (Sheldon, unpublished field notes). They have been breeding residents on Santa Catalina, Santa Cruz, and Santa Rosa since at least 1968, and possibly since at least 1947 on Santa Cruz.

None of the groups of observers who visited San Miguel prior to 1968 recorded Allen's Hummingbird. Since 1968 this species has been a common breeder there.

The conspicuous Acorn Woodpecker was unrecorded from any island until it invaded Santa Cruz some time between 1927 and 1930 (Hoffman 1931) and subse-

quently became a widespread resident breeder. It was first recorded from Santa Catalina in 1955 at the southeast end (Miller 1955), and by 1968 had spread over the southeast half of the island as a resident breeder but had not yet reached Isthmus in the north-west part, and was at Isthmus by 1973. A few individuals reached Santa Rosa in 1927, and one individual reached Anacapa in 1974, without evidence of establishing breeding populations.

As mentioned previously, the Ash-throated Flycatcher has bred in small numbers on Santa Cruz at least since 1968. It is still a migrant on all other islands, as was formerly also true on Santa Cruz.

Common Starlings (*Sturnus vulgaris*) were introduced by man to the eastern United States from Europe in the 1880's. They spread to the California mainland by 1944, reached Santa Cruz in 1964, San Clemente in 1965, and were breeding on all islands except Santa Barbara by 1968 and Santa Barbara by 1972.

The nearly-endemic island race of Orange-crowned Warbler (*V.c. sordida*) was not found breeding on San Nicolas prior to 1968, despite visits in 17 years and complete surveys in four years, including 1962-3. By 1968 about eight pairs of *sordida* were nesting, and this had increased to 20-30 pairs in 1973, and 30-40 pairs in 1974-6.

The House Sparrow (*Passer domesticus*), another European exotic introduced to the United States in the 19th century, now breeds on San Clemente, Santa Catalina, and San Nicolas. It colonized these islands between 1907 and 1915, between 1911 and 1928, and between 1945 and 1961, respectively.

Western Meadowlarks (*Sturnella neglecta*) were first recorded in 1945 on San Nicolas by Rett (1947), who found several singing in the spring and still present in the fall. All subsequent visitors have found them common, widespread breeders. Colonization must have occurred between 1940 and 1945, since none was reported on visits in 10 years between 1863 and 1940.

Like the Ash-throated Flycatcher, the Black-headed Grosbeak has bred in small numbers on Santa Cruz at least since 1968, but is only a migrant on other islands, as was also formerly true on Santa Cruz.

Rufous-crowned Sparrows (*Aimophila ruficeps*) and Chipping Sparrows (*Spizella passerina*) were first recorded on Anacapa in 1940 and have been breeding at least since 1963, though with considerable fluctuations in abundance.

TERMINAL EXTINCTIONS

The following populations bred for many years, disappeared, and have not recolonized.

Bald Eagles (*Haliaeetus leucocephalus*) formerly bred on all eight islands (nests found on seven islands, type -j and -t evidence on Santa Barbara). The last documented nesting was in 1949 on Santa Rosa (egg set in WFVZ), though birds were subsequently seen there until about 1958. Reasons for the disappearance will be discussed later.

Ospreys (*Pandion haliaeetus*) formerly bred on San Nicolas, Santa Catalina, and San Clemente. The last documented nesting was on San Clemente in 1927 (egg set in WFVZ).

Peregrine Falcons probably bred formerly on all islands except, perhaps, San Nicolas, nesting having been proved on five islands. The last documented nesting was on Anacapa in 1939 (Sumner MS). In-

and-out changes and reasons for the disappearance will be discussed later.

G. Willett found "quite a few [Bushtit (*Psaltriparus minimus*)] in the western oak region of Santa Catalina in the springs of 1904 and 1905" (Howell 1917: 100), these being the first years for which considerable ornithological information about Santa Catalina is available. Subsequent observers have not found this population again despite specific searches, although the Bushtit is still resident on Santa Cruz. Willett did not comment on the breeding status of this species on Santa Catalina. However, his observations probably pertain to a former breeding population rather than non-breeding vagrants, because: (a) the Bushtit is one of the most sedentary North American bird species, never having been recorded from any other California island (including Farallones) except Santa Cruz, where it breeds, and Anacapa (one record); (b) the oak woodlands of Santa Catalina are typical of the habitat in which the Bushtit breeds on Santa Cruz and the California mainland; (c) quite a few were seen in two successive years.

Endemic races of the Bewick's Wren (*Thryomanes bewickii*), Rufous-sided Towhee (*Pipilo erythrophthalmus*), and Song Sparrow (*Melospiza melodia*) were formerly common residents of San Clemente but disappeared due to habitat destruction by goats. The first disappeared by 1968, the second at least by 1976, and the third in 1973. An unmated male Bewick's Wren that was observed in 1973 and captured and photographed in 1974 apparently did not belong to the endemic race and may have been a vagrant from another population (Stewart et al. MS). Populations of Song Sparrows and of House Finches disappeared from Santa Barbara between 1959 and 1968 following habitat damage by rabbits and a fire.

Hooded Orioles (*Icterus cucullatus*) may have bred regularly on Santa Catalina, nesting having been proven in 1908, 1911, and 1968 and being probable in 1906. They have not bred in 1973-6.

IN-AND-OUT POPULATIONS

Most cases of turnover involve populations that alternatively breed and disappear for varying numbers of years. Each of these populations generally comprises only a small number of individuals and remains subject to high risk of extinction, for one or more of several reasons: (a) the island is very small (cf. numerous cases cited below for Anacapa and Santa Barbara); (b) the island is large, but the species requires a very large territory (cf. cases of the large hawks and owls cited below); (c) the island is large but the species occupies a specialized habitat (cf. cases of American Coot and Red-breasted Nuthatch [*Sitta canadensis*]); (d) the island is large, and suitable habitat is extensive, but the species' numbers are severely limited by the presence of a competitor (cf. several cases involving hummingbirds). On the smaller islands a majority of the populations may be in-and-out populations: for instance, of the 17 species recorded as having bred in the past 78 years on San Nicolas, 12 are known to have exhibited

turnover there. In-and-out changes are the major source of error in long-term turnover studies, because two surveys at an interval of more than one year may find a species either present in both years or else absent in both years but cannot reveal the number of intervening extinctions and immigrations. For instance, an observer who visited San Nicolas only in 1968 and 1974 would have found Northern Mockingbirds breeding in both years; one might have assumed no turnover, and remained unaware of the four cases of turnover that actually intervened (an extinction between 1968 and 1969, immigration between 1971 and 1972, extinction between 1972 and 1973, and immigration between 1973 and 1974). As shown in figure 3, and as is discussed in more detail by Diamond and May (in press), the in-and-out effect causes apparent turnover rates calculated from surveys several decades apart to be underestimates of the true value by approximately an order of magnitude. As further yearly surveys of the islands have become available, it is becoming clear that many populations considered to be regular breeders or to have undergone terminal immigration or extinction are actually participating in in-and-out turnover. The known examples follow:

The Red-tailed Hawk nested on Anacapa in 1927 (Pemberton 1928); was not even present in 1910–12; did not nest in 1968 or 1974, when only stray individuals were seen on one or two occasions, nor probably in 1970; and the status is uncertain for 1939, 1973, 1975, and 1976, when apparently territorial, vocal pairs were present but a nest could not be located. Several pairs nested on San Clemente in 1907 (Linton 1908) but not in 1897, probably not in 1915, and not in 1968 nor 1973–6. On San Miguel it did not nest in 1938–9 (Sumner MS). One or two pairs were resident there in 1968, 1972, 1973, 1975, and 1976, and nesting occurred in at least one of these years, but it is unclear exactly when and how often turnover occurred.

The Peregrine Falcon bred on Santa Barbara in 1908 (Howell 1917) but was not observed in 1897 during a 6-day stay by Grinnell (1897), and could hardly have been overlooked if it had been present on this tiny island. It bred on San Clemente in 1907 (Linton 1908) and 1915 (Howell 1917), but was not found in 1897 during 7-day and 11-day stays by Grinnell (1897), although his camp was less than 3 km from a 1907 nest site.

Bald Eagles bred on Santa Barbara in 1911 and 1912. It is possible but not certain that they failed to breed there in 1897, when Grinnell's (1897) sole observations for his 6-day visit read, "seen on two occasions flying over the island."

A pair of American Coots bred on Santa Cruz in 1922 in the marsh at Prisoners Harbor (Dickey and van Rossem 1923), but there are no previous or subsequent indications of breeding.

A pair of Black Oystercatchers bred on Bird Rock at Santa Catalina in 1966 (Harper 1971) and 1976.

Several individuals were present north of Isthmus and on Bird Rock in the summer of 1975, but breeding evidence was not obtained. There were no records of this species for Santa Catalina before 1966 nor from 1967 to 1974, despite a careful search in the summer of 1974.

A pair of Mourning Doves (*Zenaida macroura*) bred on Anacapa in 1970, and may also have done so in 1968. Only occasional non-breeding individuals were seen in 1963, 1973, 1975, and 1976, and none at all was seen before 1958 nor in 1974.

Because Barn Owls are nocturnal and easily overlooked, we have made no assumption of turnover on any island. However, turnover probably has occurred at least on Santa Barbara, where there were no records before 1968 but up to eight owls present in each survey year from 1968 to 1976. Breeding was proved in 1975. Breeding has also been proved recently on San Miguel and Santa Catalina.

Similar difficulties arise in documenting turnover of Burrowing Owls, but evidence is available for Santa Barbara and San Nicolas. On Santa Barbara three to six pairs were resident, seen virtually daily, and regularly flushed from burrows in 1968, 1972, and 1973. There were one or two pairs in 1974, and two pairs in 1975 and 1976 (type-s and -t breeding evidence). The species was not found on this small island until 1927 despite active searches for it, was scarce or absent in 1950 and 1958, and common from 1953 to 1957. On San Nicolas in 1963, Townsend (1968, amplified by personal communication) found a year-round population and a defended burrow (type-s and -t breeding evidence). There are also records of uncertain breeding significance for 1886 and 1945. However, the sole San Nicolas records for 1968, 1973, 1974, and 1975, despite a total of 36 visits and over 1000 hours of field observations by Jones, Schreiber, Diamond, and others, were of single sightings in October 1974 and September and November 1975. Several individuals were seen between January and May 1976, but all had left by mid-May. Thus, one extinction between 1963 and 1968 may be assumed conservatively. Breeding has also been documented on Santa Catalina and San Clemente.

A pair of Long-eared Owls (*Asio otus*) nested on Santa Catalina in 1909 and probably again in 1910 (Howell 1917). Since night observations by residents and visitors on Santa Catalina since 1968 have proven breeding of three owl species and frequently detected two non-breeding caprimulgids, the lack of any records for Long-eared Owl since 1910 is considered significant and constitutes evidence of extinction.

At least one Anna's Hummingbird bred, or attempted to breed, on San Clemente in 1915 (type-m evidence, see p. 546 for details; Howell 1917) but not previously or since. It is probably limited by competition from the much commoner resident Allen's Hummingbird. (Both species breed on Santa Catalina and Santa Cruz, but Anna's is much less common). Costa's Hummingbird probably bred on San Miguel in 1968, where Allen's is common, but conclusive evidence is lacking. There are no records of Costa's Hummingbird on San Miguel in other years. It bred on Santa Barbara in 1911 (Willett 1912) but was not recorded in 1897, and there has been no indication of breeding there in the past nine years.

One pair of Black Phoebe (*Sayornis nigricans*) nested on Anacapa in 1970, but in no other year except possibly 1941 (specimen collected in March and labelled "breeding"). An unfinished nest was found on San Clemente in 1907 (Linton 1908), but there

are no breeding-season records for other years despite thorough searches of all available habitat in 1968 and 1973-6, including the area where Linton found the 1907 nest.

On Anacapa, the Horned Lark (*Eremophila alpestris*) was one of the three commonest land birds in June 1910; breeding was documented in 1927 and 1932 (egg sets in WFVZ); several were seen in 1934, but no other details are available; none was found in April 1939 or May 1940; a breeding male was collected in 1941; none was observed in 1962, 1963, or 1968, and only one uncertain record in 1964; several territorial pairs were flushed underfoot from apparent nest sites in April and May 1970; and none bred in 1973-6. Thus, one must assume at minimum an extinction after 1932, an immigration between 1968 and 1970, and another extinction between 1970 and 1973.

One pair of Barn Swallows nested on San Nicolas in 1975 and 1976, but the species had not been recorded even as a migrant until September 1973. On Santa Barbara either one or two pairs bred in 1975 (type-m and -t evidence) and probably bred in 1912, but not in 1897, 1968, 1972, 1973, 1974 or 1976. On San Clemente a few have been present locally in each summer and bred in at least some summers since 1968, and possibly bred in 1915, but were not seen in other years before 1915.

One pair of Common Ravens (*Corvus corax*) nested on Anacapa in 1911 (Burt 1911.) and possibly in 1939; records for other early years are lacking; none was present in the 1963, 1964, 1968, 1973 or 1976 breeding seasons; and one or two individuals were resident during the 1970, 1974 and 1975 seasons, but breeding was doubtful. Ravens bred on San Miguel in 1939 (Summer MS) and probably in earlier years, but none has been seen in recent years. On Santa Barbara ravens were recorded by at least five observers between the 1860's and 1939, bred on at least some occasions, were not seen by Wright and Snyder (1913) in 1912, and did not breed in 1968 or 1972-6.

Red-breasted Nuthatches and possibly Cooper's Hawks (*Accipiter cooperii*) nested in the pine forest of Santa Cruz in 1911 (Howell 1917). The nuthatch was present and apparently breeding in the summers of 1971 and 1976, absent in other recent summers.

One pair of Northern Mockingbirds bred on San Nicolas in 1968, 1972, 1974, 1975 and 1976, but not in 1963 or any earlier survey year, nor in 1969, 1970, 1971, or 1973.

An American Robin nest was found on Santa Cruz in 1935 (E. Harrison, pers. comm.; Badger, unpubl. field notes in WFVZ).

At least one pair of Swainson's Thrushes (*Catharus ustulatus*) nested on Santa Catalina in 1976 and possibly also in 1963 at Eagle's Nest, which supports the lushest riparian vegetation on the island. In 1968, 1973, and 1975 we and other observers searched the Eagle's Nest area frequently but did not find this thrush in the breeding season.

One pair of Loggerhead Shrikes (*Lanius ludovicianus*) nested on Santa Barbara in 1906 (WFVZ). A pair nested on Anacapa in 1899 (Willett 1912), 1973 and 1976, and one or two pairs probably in 1968, but none in 1906-12, 1934, 1939, 1963, 1964, 1974, or 1975. One pair bred on San Miguel in 1973, probably also in 1968 and 1975, and possibly in 1976, but there are no records for earlier years.

A territorial pair of Hutton's Vireos has been found in a wooded canyon of West Anacapa on all visits to this canyon for the past four years (March, August, and November 1973, March 1974, March and August

1975, and August 1976). There are no earlier records for Anacapa, although this same canyon was checked frequently. Hutton's Vireo is generally sedentary and not migratory, so that these birds are unlikely to be winter visitors or migrants. Because the National Park Service forbids landing on West Anacapa between mid-March and early August in order to protect the Brown Pelican colony, we have not witnessed breeding in this case. We infer a breeding pair from singing, territorial behavior, and prolonged residency of this sedentary species.

One pair of Orange-crowned Warblers bred on Santa Barbara in 1975, and probably in 1939 (Hunt and Hunt 1974), but not in 1968, 1972, 1973, 1974, or 1976; nor did visits before 1939 or in 1953 through 1958 provide any indication of breeding.

Pemberton (1928) found a colony of House Sparrows in 1927 on Santa Rosa. The population persisted at least until 1951 but has more recently been absent (at least since 1968). There have been no records on Santa Cruz since a sighting in 1915 (Dawson 1915).

A colony of up to 40 pairs of Red winged Blackbirds (*Agelaius phoeniceus*) bred on Santa Cruz from at least 1968 until 1975 in willows and cattails at Prisoners Harbor, where one individual was also collected in 1948. None of the numerous earlier observers on Santa Cruz found this species, although many of these observers used Prisoners Harbor as their base. It did not breed in 1976.

Lesser Goldfinches (*Carduelis psaltria*) bred on Santa Rosa in 1927 (Pemberton 1928), 1974, and probably 1976, but not in 1968 or 1973.

"FLUKES"

In the following three cases a species which a priori must have been considered unlikely to colonize a certain island nevertheless did breed there one year, disappeared the following year, and has not bred since. State bird lists provide numerous examples of the mainland analogues of these island flukes.

Lesser Goldfinches breed in woodland and arborescent chaparral on Santa Cruz, Santa Catalina, and (intermittently) on Santa Rosa, and frequently reach other islands without breeding. Because San Miguel lacks such habitats, is relatively barren, and has practically no vegetation over 2 m high, San Miguel would have been considered unsuitable for breeding of this species. Nevertheless, one pair nested in May 1975 in open *Baccharis*-grassland habitat.

Brewer's Blackbird (*Euphagus cyanocephalus*) has often reached all the islands as a spring or fall migrant. The sole breeding on any island is for San Nicolas in 1963 and possibly 1962, when a group of at least two pair nested (Townsend 1968).

White-crowned Sparrows (*Zonotrichia leucophrys*) winter abundantly on all the islands. There are no records of breeding nor indeed of summer residency except for San Nicolas in 1963, when Townsend (1968, amplified by personal communication) observed small numbers resident through the summer in the east-central part of the island, including fledglings being fed by adults. The White-crowned Sparrow breeds in similar habitats on the mainland coast, but this record represents a temporary southward range extension of about 120 km.

DISCUSSION

EFFECTS OF MAN ON TURNOVER

Much of Johnson's (1972) and Lynch's and Johnson's (1973, 1974) criticism of published turnover studies focuses on effects of man. These authors argued that man, by modifying habitats and eliminating bird populations, has inflated turnover rates well beyond the values that would otherwise have been observed. The actual problem is more complex: man has acted both to increase and to decrease turnover, in several direct and indirect ways, some immediately obvious and some less obvious. Man's most direct effects have been the introduction of populations to islands, and the elimination of native populations by shooting and other means. Less direct effects have been mediated by man's destroying, creating, or modifying habitats; by directly or indirectly increasing or decreasing the mainland pool of potential colonists; and, perhaps most important in the long run, by shifting the balance, through these various effects, between high-turnover and low-turnover populations on an island. As a model for understanding how these different effects may either increase or decrease turnover, consider the small area of pine forest on Santa Cruz, where the Red-breasted Nuthatch breeds intermittently but turns over because it cannot build up a sufficiently large population to survive for long. If man destroyed such a forest, or created a forest on an island initially lacking one, the immediate effect would be to inflate turnover by one case, the nuthatch's terminal extinction or terminal immigration, respectively. In the long run the effect on the turnover rate of the island avifauna would variously be: if a small forest were destroyed, to decrease turnover (by eliminating a rapidly turning over population); if a small forest were allowed to expand in area, to decrease turnover (by increasing the nuthatch's population and reducing its risk of extinction); if a small or large forest were created on an island initially without one, similarly to increase or decrease turnover, respectively. (Recall that a fauna's turnover rate T , expressed as percentage of the breeding species turning over per year, is the number of cases of turnover per year divided by the average number of species S breeding in a single year: see eq. 1, p. 539. Addition of species that do not turn over decreases T by increasing S .) If man exterminated nuthatches or introduced a nuthatch species on the mainland, the long-term effects on turnover could again be either an increase

or a decrease, depending on the forest's extent. As will be seen from the following examples, man's long-term effect on the Channel Islands avifauna has been disproportionately to eliminate high-turnover populations and to create low-turnover populations. The types of human effects are as follows:

1. *Direct introduction of species to islands.* Man has successfully introduced California Quail (*Lophortyx californicus*) and other game species to several islands: one species each to three islands, two species each to two islands. These introductions have no direct effect on calculated turnover because we do not count them as immigrations. They might have an indirect effect by competing with native populations and potential immigrants. The indirect effect of introduced species must be enormous on Hawaii but is slight on the Channel Islands, where introductions have been few, relatively unsuccessful, and confined to one bird guild. The native population or potential immigrant most likely to be affected by competition from the introductions is the California Quail itself, but it is a weak flier of which no vagrants have even reached an island, and its sole apparently native island population (on Santa Catalina) may have been introduced by Amerindians (Johnson 1972).

2. *Direct elimination of species from islands.* Populations can be eliminated directly by shooting, egg collecting, poisoning, destruction of nests, use of pesticides, and release of predators, as opposed to indirectly by changes in habitat. The only clear examples among land and fresh-water bird populations of the Channel Islands involve the terminal extinctions of the Bald Eagle, Peregrine Falcon, and Osprey from all islands on which they formerly bred as well as from the southern California mainland. These extinctions are surely due somehow to man, but the exact causes are inadequately understood. While the widespread use of insecticides after 1947 was probably the final blow to the eagle and falcon, both seem to have been declining in numbers before then. Ospreys had become generally rare in California by 1944 (Grinnell and Miller 1944), last bred definitely on the Channel Islands in 1927, and probably lingered on the islands only until the early 1930's, long before introduction of insecticides. Various islands now have feral cats and rats, and Banks (1966) speculated about their relevance to temporary declines (not extinctions) in Rock Wrens (*Salpinctes obsoletus*) and House Finches on Anacapa, but there is no evidence to support this speculation.

3. *Additions to the mainland species pool.* The Common Starling, House Sparrow, Rock Dove (*Columba livia*), and Spotted Dove (*Streptopelia chinensis*), which were released in North America by man and now breed in California, have colonized 8, 4, 1, and no Channel Islands, respectively. An indirect addition to the southern California mainland pool is the Brown-headed Cowbird (*Molothrus ater*), which was virtually absent from the Pacific slope of southern California in 1900 but had become common by 1930 in association with agriculture. To our knowledge it has never bred on a Channel Island. The latter three species make no contribution to our turnover calculations (because the Rock Dove may have colonized its sole island of breeding, Santa Catalina, before the first bird survey), while the Common Starling has contributed eight terminal immigrations, the House Sparrow three terminal immigrations and (on Santa Rosa) one in-and-out cycle. The 11 populations that have contributed no further turnover since their initial immigration are all sufficiently well established now that they seem also unlikely to contribute to turnover in the near future. Thus, the immediate effect of these mainland pool additions was to generate cases of turnover, but the long-term effect thereafter has been to reduce avifaunal turnover rates for each island, by diluting the island avifauna with zero-turnover species.

4. *Eliminations from the mainland species pool.* Three members of the island avifauna have been virtually eliminated from the southern California mainland pool since the first thorough island bird surveys in 1897: Bald Eagle, Peregrine Falcon, and Osprey, as discussed above. Elimination of these large raptors from the species pool had the immediate effect of inflating turnover through terminal extinctions, but the effect on turnover in the long run has been opposite. These raptors, like other predatory species or large species, were present on the islands in much lower number than species at lower trophic levels or species of smaller size. On smaller islands there were never more than a few breeding pairs, often only one pair, of each large raptor species. Even on an island as large as San Clemente (145 km²) Linton found only two pairs of Peregrine Falcon in 1907. As we will show, extinction rates increase steeply with decreasing population size (figure 6). Hence, one would expect the large raptors to have had exceptionally high turnover rates, as discussed by Hunt and Hunt (1974) and Jones (1975).

This prediction is confirmed by the numerous in-and-out cycles that have been observed for large hawks and owls on the Channel Islands. In-and-out cycles were recorded for Peregrine Falcon, Red-tailed Hawk, and possibly Bald Eagle on one or more islands even before 1915, and the absence of annual surveys at that time makes it likely that many other in-and-out cycles went undetected. The effect on turnover of eliminating the three large raptors has therefore been, in the long run, to remove one of the most rapidly turning-over groups in the island avifauna, and to reduce turnover by all the in-and-out cycles that the raptors would have undergone if they had not been eliminated.

5. *Terminal extinctions or immigrations due to habitat changes.* Some terminal extinctions or immigrations may be direct consequences respectively of man's destroying or creating habitats. As background for identifying such cases on the Channel Islands, recall that each Channel Island was hardly in pristine condition at the time of the first thorough bird survey (some year between 1897 and 1939, depending on the island). Before Europeans arrived, the islands had been inhabited for at least 12,000 years by Amerindians (Orr, in Philbrick 1967), who may have eliminated the Channel Islands population of the extinct flightless duck (*Chendytes lawi*; Morejohn 1975). Grazing animals had been introduced to all islands by Europeans at least by the first half of the 19th century, possibly earlier on most islands. Records of the number of sheep or goats maintained, and accounts of early pioneers, show that grazing on many islands was heaviest in the mid-19th century. Thus, transformation of large areas from chaparral and woodland to grassland or sparse shrubs had been accomplished long before the first bird surveys. The problem is therefore to recognize *changes* in habitat between the surveys that could underlie *changes* in bird populations. Comparison of the islands as we see them now with photographs and descriptions at the times of the first thorough bird surveys suggests the following changes, as summarized from a detailed account (Jones 1975 and in prep.). San Nicolas and San Miguel, which were already rather barren at the first survey, remain relatively barren despite termination of grazing within the last three decades. Santa Cruz, Santa Rosa, and Santa Catalina, the three largest and most heavily wooded islands, retain the same mix of habitats as on first survey and still have grazing, though now more carefully managed than be-

fore. San Clemente, already stripped of most of its chaparral before the first survey, has experienced further reduction of understory thickets in the few ravine woodlands, due to goats. Between 1918 and 1959 farming, rabbits, and a fire destroyed most thickets on Santa Barbara, the island most changed between surveys. On Anacapa termination of grazing in the 1930's has permitted scrub to expand at the expense of grassland and ice plant (*Gasoul crystallinum*), but extensive areas of the latter habitats remain.

Five terminal extinctions and one terminal immigration are obviously the result of habitat alteration by man, as discussed previously in the text: extinctions of the House Finch and Song Sparrow on Santa Barbara, and of the Bewick's Wren, Rufous-sided Towhee, and Song Sparrow on San Clemente, due to habitat damage; and immigration of the American Coot to Santa Catalina, due to habitat creation. These appear to us the only cases in which man-induced habitat alteration has played a decisive role in terminal immigration or extinctions, but several other types of cases warrant discussion: (1) Banks (1966), in comparing the breeding avifauna he found on Anacapa in 1963-4 with that found by earlier observers, attributed the decline and (as he believed) extinction of the Horned Lark, and immigration of the Rufous-crowned and the Chipping sparrows, to reduction in grassland and expansion of scrub. This interpretation seems at most only partly correct. Anacapa still has approximately 40 ha of habitat similar to that in which Horned Larks are abundant on San Nicolas and Santa Barbara, and Horned Larks recolonized and bred on Anacapa since Bank's visit. Our censuses of 1968-1976 reveal large year-to-year fluctuations in numbers of the two sparrows, both of which nearly disappeared in 1976 despite continued expansion of scrub. On an island as small as Anacapa, even the most abundant species has such a small population that turnover due to year-to-year population fluctuations unrelated to habitat succession is high. (2) Man may have contributed in several ways to extinctions of the Common Raven on the three smaller islands (Anacapa, Santa Barbara and San Miguel). However, interpretation of these extinctions remains unclear, because ravens continue to breed abundantly on the remaining five islands in the presence of man; breeding on Anacapa and Santa Barbara may formerly have been intermittent rather than annual; and in recent years ravens have been

seen on Anacapa and Santa Barbara and have intermittently been summer residents of doubtful breeding status on Anacapa. (3) Some terminal immigrants use both natural and man-made nest sites, and have had access to the latter since long before the first bird survey. For instance, nests of Barn Swallows on the islands are usually in natural sea caves, though sometimes on buildings or piers. Barn Owls on the islands usually nest on cliffs, though perhaps sometimes on buildings. No change of conditions between earlier and later surveys is involved. (4) Some terminal immigrants use both natural and man-made habitats. For example, the Killdeer, which colonized three islands, usually requires proximity of fresh water for breeding. On Santa Rosa and Santa Cruz it breeds only in natural habitats (along streams); on Santa Catalina, in natural habitats (along streams, along the coast, and on Bird Rock) and also near several man-made reservoirs.

Assessment. We accept 119 cases of turnover as having occurred since the first reasonably complete bird surveys in 1897, counting each immigration or extinction as one case. Of these, about 33-39 cases, or 27-33% of the total, can be attributed to the effects of man, depending on how one assesses the three Anacapa cases and the three raven cases discussed above. The man-related cases include 9-11 of the 37 terminal immigrations, and most (23-26 out of 33) of the terminal extinctions, but only 1 or 2 of the 43 in-and-out changes and none of the six fluke changes. However, these figures greatly exaggerate the contribution of terminal immigrations and extinctions to total turnover, because comparison of surveys up to 79 years apart detects all terminal extinctions and immigrations but overlooks about 90% of the in-and-out changes (fig. 3). A better assessment can be made by considering only those cases of turnover since 1968, because the shorter intervals between surveys (one to at most five years) mean that fewer in-and-out changes escaped detection. Of the 29 cases detected between 1968 and 1976, only four (immigration of the Common Starling to Santa Barbara, extinction of the Bewick's Wren, Rufous-sided Towhee and Song Sparrow on San Clemente) involve effects of man. The conclusion that turnover measured at short intervals is less affected by man than turnover at long intervals is hardly surprising. However, the real problem with long-time-base studies is not that they inflate turnover rates by a factor of about 1.5 due to effects of man, but that they underestimate turnover

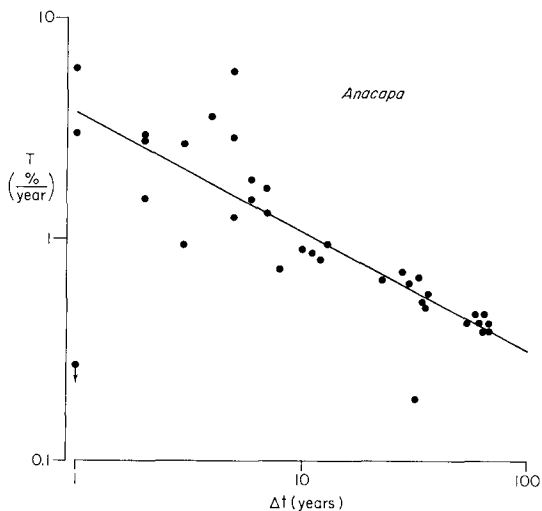


FIGURE 3. Turnover rates were calculated for Anacapa Island by eq. 1, from comparison of breeding lists in the survey years listed in the text and taken in all pair-wise combinations. Ordinate: turnover rate T (%/year); abscissa: interval between surveys Δt (years). Scales are logarithmic. The point with an arrow denotes a pair of surveys at an interval $\Delta t = 1$ that exhibited zero turnover. Note that T decreases with Δt , because of the in-and-out effect.

rates by a factor of about 10 due to overlooked in-and-out changes (next section). Annual censuses minimize this problem. Man's overall effect on the species pool has been to remove three rapidly turning-over species and to inject two non-turning-over "regular breeders." Because of this transformation of the pool, the turnover rates revealed by annual censuses within the past decade may be lower than those that would have been observed early in this century.

TURNOVER VALUES

For each island and for each pair of years in which a reasonably complete survey was available, we calculated relative rates of avifaunal turnover, T , based on the 119 cases of turnover discussed on pp. 532–535. T was calculated as

$$T = 100 (I + E) / \Delta t (S_1 + S_2) \quad (\text{eq. 1})$$

where S_1 and S_2 are the number of breeding species in the earlier and later survey year respectively, I and E are respectively the number of immigrations and extinctions based only on comparison of the lists for the two years (i.e., ignoring any known in-and-out changes in the intervening years), and Δt is the number of years between the two surveys. The factor 100 in eq. 1 means that the units of T are %/year; i.e., the percentage of the island's

breeding species that are replaced by other breeding species per year. Unresolved questions of breeding presence or absence were evaluated conservatively with respect to conclusions of turnover, as discussed on pp. 528–529. Thus, the resulting turnover rates are minimum estimates for two reasons: conservative evaluation of species lists for the survey years, and neglect of in-and-out changes between survey years.

Figure 3 plots these apparent values of T against Δt on a double logarithmic scale for Anacapa, using all pair-wise combinations of survey years and fitting a straight line through the points. Apparent T values decrease by an order of magnitude as the survey interval Δt increases from 1 year to several decades. From the fitted line of figure 3, the "true" value of T for Anacapa—i.e., that measured at one-year intervals—is 3.7%/year. The apparent value measured at the longest survey interval ($\Delta t = 67$ years) is only 0.41%/year. The reason for the decrease in T with increasing Δt is that more cases of undetected in-and-out changes are completed within longer intervals. Thus, the in-and-out effect causes surveys performed at an interval of several decades to underestimate turnover by approximately an order of magnitude. Diamond and May (in press) provide examples from other island avifaunas, and show how the decline in apparent turnover rate and also in its statistical fluctuations with time, as illustrated in figure 3, is related mathematically to the immigration and extinction probabilities of each breeding species.

Figure 4 depicts the number of breeding species S on each island in each survey year. The number written over the line connecting each pair of surveys is the percent turnover (not turnover rate), defined as $100 (I + E) / (S_1 + S_2)$ and meaning the percent of the avifauna that turned over between surveys. Several points can be noted from figure 4:

On no island is S perfectly constant (ordinate values of figure 4). However, the fluctuations in S are relatively small. The sole instance in which the change in S between surveys exceeds 25% of S 's initial value is between 1910 and 1968 on Santa Barbara, where S declined by 36% due to the fire-related excess of extinctions. S fluctuates relatively more on the smaller, more species-poor islands (Anacapa, Santa Barbara, San Miguel, San Nicolas: average $S = 9$ –17 species, $A = 2.6$ –58 km²) than on the larger, more species-rich islands (Santa Cruz, Santa Rosa, Santa Catalina, San Clemente: average $S = 23$ –38 species, $A = 145$ –249 km²). Excluding the 1910–

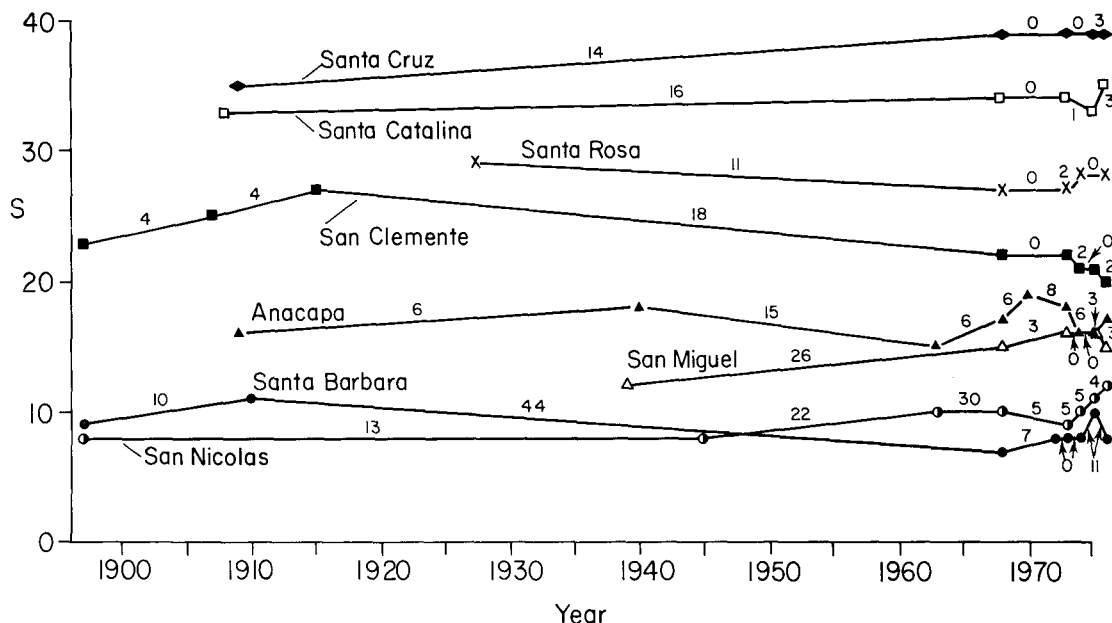


FIGURE 4. Fluctuations in number of breeding species S for each island (ordinate). The abscissa is the survey year. The number written over the line connecting each pair of the points is the percent turnover between surveys (not turnover rate).

1968 interval on Santa Barbara, the average magnitude of change in S (irrespective of sign) between surveys is 11% on the small, species-poor islands, 4% on the large, species-rich islands. We interpret this effect as the expected increase in statistical variability, as population sizes and species numbers decrease with decreasing area. These increased temporal fluctuations in S on small islands are the counterpart of the increased spatial fluctuations noted previously; if one compares S on islands of similar area censused in the same year, the coefficient of variation increases with decreasing area (Diamond 1974, Diamond and Mayr 1976).

There is considerable turnover in species even when S itself is the same or nearly the same in two successive surveys. The only instances in which there is no turnover between surveys are in some short intervals of 1–5 years. Three pairs of successive censuses reveal turnover despite no change in S : San Nicolas, 1897–1945, turnover 13%, S constant at 8; San Nicolas, 1963–1968, turnover 30%, S constant at 10; Santa Cruz, 1975–1976, turnover 3%, S constant at 38. On Santa Catalina between 1908 and 1968, S was nearly constant (33–34), but turnover was 16%.

The relative constancy of S in the face of turnover is in accord with the MacArthur-Wilson hypothesis that species number on an island may track an equilibrium value. Non-equilibrium trends in S appear only for Santa

Barbara (net loss of 4 species due to fire) and San Clemente (net loss of 7 species since 1915, partly due to habitat damage by goats). Even for these two islands, in-and-out turnover has been superimposed on the net decline, as several extinctions were offset or reversed by immigrations.

Average values of apparent turnover rates, calculated by averaging values obtained from all pairs of successive censuses on each island, are 0.5–1.0%/year for the four larger islands, 1.2–3.6%/year for the four smaller islands. Values calculated only from the one-year survey intervals of the period 1973–1976 are higher (0.9–1.9%/year and 1.6–5.6%/year for the larger and smaller islands, respectively) and are more meaningful, because errors produced by the in-and-out effect at long survey intervals are avoided. Our best estimates, the one-year values estimated by the curve-fitting procedure of figure 3, are similar: 0.5–1.4%/year and 0.8–4.9%/year for the larger and smaller islands, respectively. For almost all islands, these values (based on more surveys than Diamond [1969] used in his turnover calculations) are considerably higher than his values (0.3–1.2%/year), his underestimates being greatest for the islands with the highest turnover rates. The reason for Diamond's underestimations is that his survey interval was 51 years, so that the in-and-out effect lowered his apparent T values below the true ones, as illustrated by figure 3.

We know of two other published analyses of bird turnover based on annual censuses. Both are based on smaller islands or sample areas than any Channel Island, and both involved longer series of censuses than available for the Channel Islands. From 29 consecutive annual breeding censuses of the Farne Islands (total area $\sim 0.3 \text{ km}^2$) off Great Britain, Diamond and May (in press) calculated $T = 13\%/year$. From analysis of 48 consecutive annual breeding censuses in Trelease Woods in Illinois by Kendeigh, Whitcomb et al. (1976) obtained $T = 14\%/year$.

The above figures all refer to *relative* turnover rates, the percent of an island's avifauna turning over per year. *Absolute* turnover rates (the number of species immigrating or going extinct each year) are on the average 0.28 species/year for the larger Channel Islands and 0.37 species/year for the smaller islands.

From their equilibrium theory, MacArthur and Wilson predicted that absolute turnover rates should decrease with area and also with distance. Their theory predicts that relative turnover rates should decrease even more rapidly with area than do absolute turnover rates (because relative rates equal absolute rates divided by S_{eq} , which increases with area); but that relative turnover rates should decrease less rapidly with distance than do absolute turnover rates or even remain unchanged (Williamson in press).

How well do our Channel Islands results fit these predictions? (1) Regarding the area effect, the prediction is confirmed that absolute turnover rates should decrease with area (0.37 and 0.28 species/year on the average for the smaller and larger islands, respectively), and that relative rates should decrease even more rapidly (3.2 and 0.9%/year, respectively). (2) The prediction regarding the distance effect is not confirmed: the most remote island, San Nicolas, has the highest relative and second highest absolute turnover rate rather than a low rate. We suggest two possible explanations. First, even San Nicolas's distance from the mainland (98 km) is trivial compared to the dispersal abilities of most California species that do cross water gaps. (Naturally, this does not mean that distance is trivial for all California species. Some abundant species of the mainland, such as those named on p. 531, are stopped so effectively by even the narrowest island-mainland gap of 20 km that they have never reached any island). Second, Brown and Brown (in press) point out that turnover rates should at first increase rather than decrease with increasing distance,

due to a "rescue effect": extinction rates should increase with distance because distant islands will receive fewer immigrants that might rescue a dwindling population from extinction. Brown and Brown confirmed the reality of this effect in studies of arthropod turnover on thistle "islands." (3) The above predictions tacitly assume that habitat diversity is closely correlated with area and possibly distance, so that habitat diversity does not appear as an additional variable. This assumption fails for the Channel Islands: A and d alone are only fair predictors of S_{eq} , because much variation in habitat diversity is independent of A and d (Power 1972). For instance, wooded Anacapa has twice as many breeding species as the barren and equal-sized Santa Barbara, and more species than the barren and much larger San Miguel and San Nicolas. In archipelagoes where habitat diversity independent of A and d increases S_{eq} , it presumably also has some effect on turnover rates. However, our data do not suffice to show what this effect is.

WHICH POPULATIONS ARE TURNING OVER?

Figure 5 compares, for the large islands and small islands, the estimated breeding population sizes of all Channel Island bird populations, divided into three categories: those that have bred continuously without turning over, those that bred some time in the past but are now extinct, and those that were absent some time in the past but now occur. As one would expect, the species-abundance relation for non-turning-over populations is skewed toward large populations on large islands but not on small islands. The median size of these populations is about 50 pairs on the large islands but only 5 pairs on the small islands. On both the large and small islands, both the immigrant populations and the extinct populations are disproportionately drawn from the small populations, and their species-abundance relations are sharply skewed to the left.

Figure 6 illustrates how steeply the risk of extinction declines with population size. Only one population that exceeded 100 pairs became extinct on any Channel Island in this century, while 39% of the populations that numbered less than 10 pairs became extinct in the same period. Conversely, only six of the immigrant populations succeeded in achieving a population size over 100 pairs, and most either became extinct or else have fluctuated tenuously between 1 and 5 pairs.

Thus, smaller populations have contributed disproportionately to turnover. Naturally, this

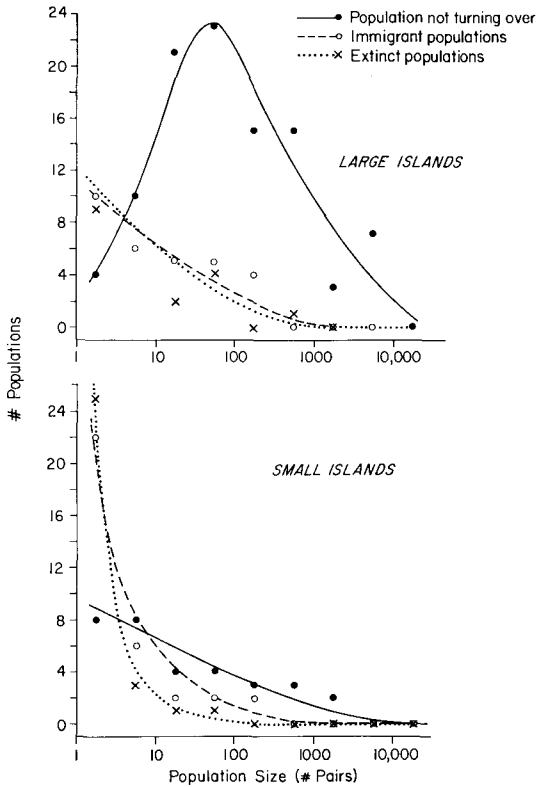


FIGURE 5. Population size and turnover on the Channel Islands. On each island the average breeding population of each species was estimated as falling into one of nine size classes (1–3 pairs, 4–10 pairs, 11–30 pairs, etc.). Populations were then grouped as to whether they immigrated, became extinct, or never turned over since the first surveys. The number of populations (ordinate) in each size class (abscissa) was summed for the four larger islands (above) and for the four smaller islands (below).

conclusion does not mean that island populations are of two sorts: small ones that are in dynamic equilibrium, and large ones that are not. Instead, figures 5 and 6 simply mean that turnover rates decrease continuously with population size.

SYNTHESIS

In this concluding section we present a model summarizing our observations on community dynamics. We find it convenient to delimit arbitrarily five stages in colonization: dispersal, commencement of breeding, saturation of carrying capacity, survival for only a short time, and survival for long times.

As illustrated in figure 7, the process begins with the dispersal of colonists to islands from the mainland or from other islands (steps 1a and 1b). Some species have never reached the islands at all (e.g., Wrentit, Red-shouldered Hawk), while other species reach every island every year in numbers.

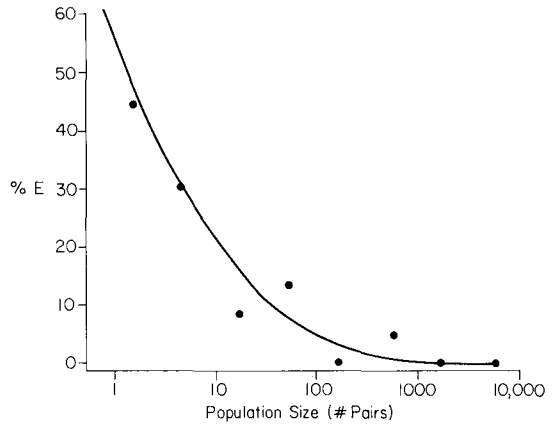


FIGURE 6. Incidence of extinction as a function of population size, calculated from the data of figure 5. For each breeding population size class (abscissa), the ordinate gives as a percentage the number of populations in that class that became extinct since the first surveys, divided by the total number of populations in that class.

Some colonists who reach the islands fail to breed, either because of the absence of suitable habitat (step 2a), or else despite the presence of suitable habitat (step 2b) but correlated with the presence of competing species, or else correlated perhaps with strong philopatry. Other colonists reach an island already occupied by a breeding population of conspecifics, into which they are absorbed (step 2c). Still other colonists find an unoccupied island with suitable habitat and commence to breed (step 2d).

The new breeding populations founded by those colonists reaching step 2d survive for varying periods of time before eventual extinction (steps 3–5). Once colonists commence to breed, the new population may gradually increase in numbers until it reaches the carrying capacity K , the number of individuals of the species that the island can support at equilibrium. Since probability of extinction decreases with increasing population size (fig. 6), many or most new breeding populations must fluctuate out of existence soon after first breeding, before the saturating population K has been reached (step 3a; many of the in-and-out-extinctions on pp. 533–535 provide examples). For most of the immigrants that survive step 3a, K is so low, often just a single pair, that even populations which reach K (step 3b) soon disappear (step 4a; see p. 533 for the numerous alternative reasons for low K , such as small island, large territory, specialized habitat, or limitations by competitors, and pp. 533–535 for numerous examples among in-and-out populations). A few immigrants do

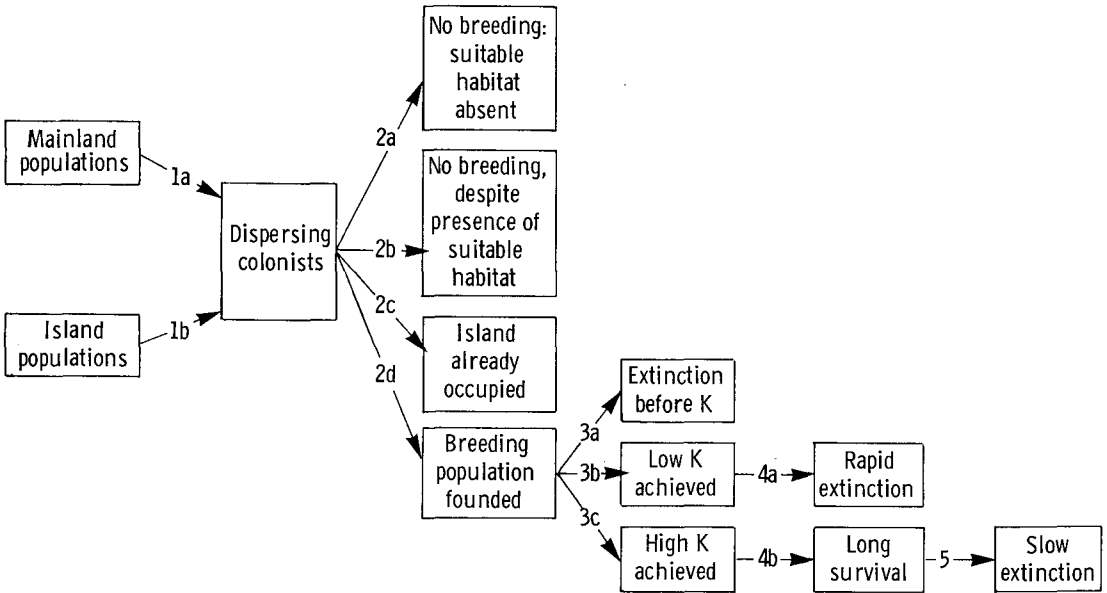


FIGURE 7. Model of stages in colonization and turnover. See text for discussion.

find an empty island with high K , succeed in achieving K , and then survive for long times (steps 4b, 5). These are the immigrants who might begin to diverge genetically and eventually might form endemic subspecies. In all, more than half of the man-unrelated immigrant populations known to have been founded on the Channel Islands since the first bird surveys have disappeared again. Most of the remainder have achieved only a tenuous existence and number less than 50 individuals, generally much fewer. Only about six natural immigrant populations (American Kestrel on Santa Catalina and San Clemente, Acorn Woodpecker on Santa Cruz and Santa Catalina, Orange-crowned Warbler and Western Meadowlark on San Nicolas) now exceed 50 individuals. These are the sole natural immigrants who succeeded in achieving K on a large island providing extensive areas of suitable habitat.

Consider the avifauna of Anacapa to illustrate how the mainland species pool becomes attenuated from step 1 to step 5. About 345 land-bird species have been recorded from the southern California mainland, of which ca. 187 breed. Of the total pool, 170 have been recorded from Anacapa, of which ca. 107 are recorded every year, the others being recorded less often than annually (step 1). Of these 107 species, ca. 73 do not find suitable breeding habitat on Anacapa (step 2a), while ca. 34 do (steps 2b–2d). Of these 34 species, on the average 17 were already breeding on Anacapa in the preceding year (step 2c). New

breeding populations have appeared on Anacapa at a rate of 0.67/year over the past decade (step 2d), but about half of these fail to survive more than one breeding season (steps 3a, 4a). Only two species have Anacapa populations that exceed 100 individuals and thus are likely to survive for a long time (step 4b).

We emphasize that the process illustrated in figure 7 is going on continually, and that a "snapshot" of an island at any moment reveals populations of different ages and at different stages of colonization. Thus, one survey of an island avifauna is like viewing "a single frame of a movie film rather than viewing the movie itself" (Levins and Heatwole 1973: 1056). Populations turn over at various rates, ranging from rapid turnover of the uncommon species or recent arrivals that account for most turnover, to very slow turnover of abundant populations. Not only do populations of different species on a given island differ in turnover frequency, but also the relative proportions of populations with different turnover frequencies differ according to island size. On a very small island most populations are small and relatively short-lived. The larger the island, the more the distribution of population ages becomes skewed to include some large, long-lasting populations (fig. 5). Thus, the proportion of endemic forms increases with island area (Mayr 1965).

In short, the practical message of our short-time-base turnover studies is that turnover calculations based on censuses spaced at long intervals reveal only the tip of an iceberg. To

obtain even approximately accurate estimates of turnover rates in bird communities requires annual surveys.

SUMMARY

Estimates of faunal turnover rates based on surveys many years apart are likely to be underestimates because of the "in-and-out effect" (a population immigrating and then going extinct, or vice versa, between surveys). Hence surveys of breeding land and freshwater bird species on the eight California Channel Islands have been carried out annually since 1973, for comparison with earlier surveys. An introductory section summarizes available sources of information on Channel Islands birds, our survey strategies, and our criteria for breeding presence or absence.

As depicted graphically by a "turnover pyramid," populations of different species on the same island fall into categories that turn over at very different rates: zero-turnover populations, consisting of either regular breeders or else of absentees (members of the mainland species pool that never breed on the island for any of five reasons); terminal immigrants, that colonized once in the survey interval and persisted; terminal extinctions, species that disappeared in the survey interval and did not recolonize; in-and-out populations, that immigrated and became extinct repeatedly; and flukes, populations that once colonized unexpectedly and soon disappeared. Numerous examples of Channel Islands populations in each category are given.

Man has acted both to increase and to decrease turnover in several direct and indirect ways. The in-and-out effect causes turnover values based on comparison of surveys several decades apart to underestimate the true values by about an order of magnitude. Conservative estimates of turnover rates for the Channel Islands, based on one-year survey intervals, range from 0.9%/year for the larger islands to 5.6%/year for the smaller islands. Relative and absolute turnover rates decrease with island area. Despite this turnover, species number on most islands has remained approximately constant because the immigration rate approximately equals the extinction rate.

Extinction rates decrease steeply with population size. Relatively few immigrant populations succeed in achieving large numbers.

On the basis of these observations, a model of the stages in colonization is proposed. Criticisms directed by Lynch and Johnson at previous turnover studies are considered in an appendix.

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APPENDIX

Johnson (1972) and Lynch and Johnson (1973, 1974) criticized Diamond's (1969) study of turnover on the Channel Islands, and Lynch and Johnson (1974) also criticized studies of turnover on Mona Island in the Caribbean by Terborgh and Faaborg (1973) and on Karkar Island in the Southwest Pacific by Diamond (1971). Lynch and Johnson claimed that they reappraised the data and critically examined the records that served as the basis for Diamond's assessments of breeding presence or absence on the Channel Islands. Their reassessment was that most instances of turnover Diamond accepted are either invalid or unproved, because of inadequate evidence for breeding presence or absence in one or both survey years compared; or, if proved, are due to direct or indirect effects of man. Johnson (1972) assumed natural turnover to be sufficiently low that one can reconstruct directions and approximate times of island colonizations several thousand years ago from present-day distributions, even for such vagile species as the Orange-crowned Warbler and the Horned Lark. Lynch and Johnson concluded that the turnover estimates by Diamond and by Terborgh and Faaborg appear severely inflated, sometimes by as much as an order of magnitude. They predicted (1974:383), "If equilibrium turnover rates are indeed as high as has been claimed in the studies cited, then changes in the species composition of *resident* insular avifaunas should be detectable within, say, 5–10 years."

The present study confirms this prediction: changes are detectable on most Channel Islands in one or two years. Diamond's previous estimates have proved to be underestimates rather than overestimates. It remains to point out examples of factual errors in the critiques by Lynch and Johnson. We list, first, errors of a general nature; next, examples of invalid statements concerning specific populations; and finally, difficulties underlying Johnson's reconstructions of historical colonizations.

GENERAL CONSIDERATIONS

(1) Among their guidelines for proving existence of turnover, Lynch and Johnson (1974: 372, column 2, lines 38–50, and p. 376, col. 2, lines 26–39) recommended that documentation of breeding populations should preferably be supported by collection of voucher specimens; asserted that "data on gonad condition [of the specimens] are important when one must decide on the likelihood of breeding versus migrant or casual

status"; and considered that, because Diamond did no collecting in 1968, "the possibility of misidentification of at least a few species cannot be dismissed." While collection of specimens is often justified in other types of studies, the reasons why specimens should not be collected in turnover studies on the Channel Islands are compelling. First, many of the populations turning over consist of one or a few pairs, so that collecting is likely to eliminate the populations and alter the outcome of the natural experiment. Second, no breeding bird species of the Channel Islands present significant problems of field identification except for female hummingbirds. Finally, as has often been pointed out, enlarged gonads fail to prove whether the collected individual was breeding on that island or was on migration (e.g., Lofts and Murton 1973). To establish turnover, it is necessary to abstain from collecting a suspected colonist, observe it repeatedly and determine whether it nests, and then examine whether it also nests in the following year.

(2) Lynch and Johnson considered it necessary to demonstrate that "the mere presence of a bird species on a given island, even if several individuals are seen during the peak breeding season, does *not* constitute strong evidence, much less 'proof', of resident status" (1974: 372, col. 2, lines 24-28; emphasis of *not* and quotes around 'proof' are by Lynch and Johnson). Their wording, italicization, and use of quotes implied that Diamond had claimed mere presence to be strong evidence or proof of residence, and that this claim required refutation. Hence they summarized records of migrants and vagrants on the Farallon Islands off northern California to support "our [i.e., their] contention that the presence of nonbreeding land birds on continental islands is the rule rather than the exception" (p. 373, col. 2, lines 16-19, also described as "our thesis" in col. 1, line 7). In fact, of course, the presence of numerous migrants and vagrants on the California coastal islands has been well known since the late 19th century, and caused Diamond in 1968 and Jones since 1973 to devote most field effort to determining breeding vs. migrant status. A by-product of our turnover studies has been the addition of 102 species to the list of migrants recorded from the Channel Islands. In addition, the presentation of Farallon records by Lynch and Johnson (1974: 373, their Table 1), as monthly totals for all nonbreeding land birds combined, gives a misleading picture of the nature of the problem. For the Channel Islands as for the Farallones, the great majority of nonbreeding individuals in the June and July totals are recorded in the first half of June and latter half of July. Many of the late-June and early-July records are of vagrants from eastern North America whose nonbreeding status is scarcely in doubt. We do not automatically assume any land bird observed in the latter half of June and first half of July to be breeding, but we do observe few species on the islands in this period that are not clearly breeding, and fewer still whose status is ambiguous.

(3) Lynch and Johnson (1974: 376, col. 1, lines 14-16) quoted Howell (1917: 5, lines 23-25) to support their contention (p. 382, col. 2, lines 49-50) that Howell's summaries do not provide a reliable data base for computing equilibrium turnover rates: "As a matter of fact, *there has been comparatively little work done upon these islands by anybody . . .*" (italics and termination of the quotation are by Lynch and Johnson). Their termination of the quotation reversed Howell's meaning, for the remainder of his sentence read, ". . . and a visit of several weeks to

any one of them is almost sure to add one or more new migrants or winter visitants to the list" (end of Howell's paragraph: Howell 1917: 5, lines 25-26). Howell's belief that a visit was likely to add new migrants or winter visitors to the lists for most islands is justified by our experience: we are still adding new migrants or winter visitors on almost every visit. Howell's implicit belief that a visit was not likely to add new breeding species also seems justified, for two reasons. First, having reexamined virtually all the original papers, specimen collections, and egg collections consulted by Howell, we find that the records of breeding species obtained by different collectors in the same or successive years on the same island largely duplicate each other, implying relatively thorough coverage of most islands. Second, except for Santa Rosa and San Miguel, the breeding species totals extracted from Howell for the other six islands in the years up to 1917 are close to those observed since 1968 (1917 total the same as 1968 for one island, slightly higher for three, slightly lower for two). This suggests that early breeding coverage of these six islands was not at all inadequate, and we pointed out (p. 526) that the motivation of early collectors resulted in far more complete coverage of breeding species than of migrants and winter visitors. For Santa Rosa and to a lesser extent San Miguel, the visits of early ornithologists were too few or brief for breeding coverage to be complete, and Howell's breeding totals are significantly below modern ones, as already discussed by Diamond (1969). Naturally, whether lack of early records for a particular breeding species on a particular island indicates absence or simply lack of observation depends entirely on the species' conspicuousness, the island's size, and the survey intensities, and we have assessed each case individually (see p. 529). However, the intensity of coverage up to 1917 provides no support for dismissing turnover estimates based on pre-1917 surveys as severely inflated, as Lynch and Johnson claimed.

(4) According to Lynch and Johnson (1974: 370, col. 2, lines 1-6), "The MacArthur-Wilson (1967) equilibrium model predicts that, other things being equal, large islands near a source of potential colonists should have (1) more species, and (2) a lower rate of species turnover than smaller, more remote islands." Half of this paraphrase is correct. It is true that large islands are predicted to have a lower turnover rate, because of lower extinction rates. However, MacArthur and Wilson (1967) predicted near islands to have a higher, not lower, turnover rate than more remote islands, because of higher immigration rates.

(5) Diamond (1969) calculated turnover by comparing his 1968 surveys with the avifauna recorded by Howell (1917), whose compilation was based mainly on field studies between 1897 and 1915. Lynch and Johnson (1974: 375, col. 2, lines 36-37) claimed that the result of this procedure is "to overestimate the turnover rate by some unknown fraction." Actually, the effect on turnover calculations of combining consecutive years into a single survey, for comparison with a later survey completed within one year, is two-fold: to tend to underestimate immigrations, but to overestimate extinctions. The two errors are thus opposite and tend to cancel. In the present paper the turnover rates we calculated mostly utilize surveys completed within one year, with 9 additional surveys based on combined observations for several consecutive years.

(6) In their first critique, Lynch and Johnson (1973) claimed, "We have reappraised the data ana-

lyzed by Diamond (Proc. Nat. Acad. Sci. U.S. 1969, 64: 57-63) and offered as support for his thesis of historically high rates of avifaunal turnover in the Channel Islands of California. Critical examination of records that supposedly document individual instances of extinction and immigration leads us to the following conclusions . . ." This claim is false, and Lynch and Johnson did not repeat it in their second (1974) paper. Of the nine islands that Diamond surveyed in 1968, Lynch and Johnson examined none of Diamond's records at all from his surveys for six islands, and for the other three islands examined only preliminary, briefly annotated species lists that Diamond precirculated to several people to elicit information and that did not attempt to provide detailed documentation of records.

STATEMENTS CONCERNING SPECIFIC POPULATIONS

Of the numerous populations for which Lynch and Johnson disputed Diamond's assessment of turnover, many have been discussed in the text of this paper, and others will be discussed elsewhere. Since space does not permit us here to rediscuss every case in the light of Lynch's and Johnson's comments, we consider seven cases to illustrate the types of errors involved in their arguments:

(1) Lynch and Johnson (1974: 377, col. 2) rejected Diamond's conclusion of an extinction of Anna's Hummingbird on San Clemente between 1917 and 1968, on the grounds that breeding was not adequately demonstrated in 1917 (code E1 in Table 3 of Lynch and Johnson) and that absence of a breeding population was not adequately demonstrated in later years. Here it is useful to quote Lynch and Johnson at length. "The inclusion of the Anna's Hummingbird . . . on the list of extinctions for San Clemente Island (Diamond 1971) appears to be yet another instance of pseudoturnover. Many of the early ornithologists who worked on the Channel Islands had visited San Clemente prior to Howell's summary. Among these were Howell himself, Breninger, Howard, Linton, Dickey, and Huey. Some of these biologists spent periods of weeks on the island during the height of the breeding season, but the only Anna's Hummingbird ever reported by any of these workers was the individual seen by Howell in March 1917 [sic]. Even though this individual appeared to be gathering nesting material (Howell 1917: 63), the fact that the species had never been noted previously, even as a vagrant, and has not been reported subsequently to breed on San Clemente implies that any possible breeding population never exceeded a very few pairs. Therefore, Diamond's failure to find this species during a few days' field work on this large (56 square miles) island cannot be accorded much weight." In these sentences Lynch and Johnson listed six visitors to the island prior to Howell's summary, implied that none of these investigators but Howell saw Anna's Hummingbird, and implied that there was some uncertainty what the individual seen by Howell was doing. First, Breninger and Howard commented only briefly on a few of the species they found, thus it is not known if they saw this species. Second, Dickey and Huey visited the island *with* Howell as a single party. Third, Howell's account of the party's observations does not state that the hummingbird "appeared" to be gathering nesting material in March "1917," but rather that it did collect bits of cotton

from the vicinity of the party's skinning table for several days in March 1915. Finally, dozens of visits and hundreds of man-hours of observation on San Clemente since 1967 have yielded only one record of a transient Anna's Hummingbird in five breeding seasons. Thus, the species is surely not breeding now, and the observations by Howell, Dickey, and Huey constitute a typical example of in-and-out turnover.

(2) Lynch and Johnson (1974: 378, col. 1) questioned extinctions of the Red-breasted Nuthatch and Cooper's Hawk on Santa Cruz: "While it is indeed possible that these species were once resident, neither has ever been shown to nest on this or any other of the Channel Islands . . ." For the Red-breasted Nuthatch, Howell (1917: 99; see also Howell and van Rossem 1911: 210) stated, "On May 1 [1911] I watched an individual excavating a nest site in a dead stub . . ." For the Cooper's Hawk the evidence is ambiguous, but Lynch and Johnson understated the case: ". . . I believe it to be resident in small numbers . . . On April 25, 1911, I saw a pair at the lower edge of the pines which acted very much as if they had a nest near by" (Howell 1917: 54; see also Howell and van Rossem 1911: 209).

(3) Lynch and Johnson (1974: 378, col. 1) questioned extinction of the Black Phoebe on San Clemente after a nesting record in 1908, on the grounds that absence in subsequent years was not established (code E2 in their Table 3). On our p. 535 we describe the recent searches for this species that provide adequate documentation of absence.

(4) Lynch and Johnson (1974: 378, col. 2) stated that Barn Swallows have never been shown to breed on Los Coronados. Howell (1917: 87) stated, "A limited number occur on the Coronados during the spring and summer, breeding in the sea caves where their nests must be frequently dampened by the spray."

(5) Regarding extinction of the Bushtit on Santa Catalina, Lynch and Johnson (1974: 378, cols. 1 and 2), concluded, ". . . the early sight records by Willett (*fide* Howell 1917) may well have involved a vagrant group which was blown to Catalina from the mainland." On p. 533 we state why this interpretation is implausible.

(6) Lynch and Johnson (1974: 380, 381) discussed in detail the published surveys of San Nicolas in 1897 and 1962-3, in the mistaken belief that "from the time of Grinnell's visit in the late 19th century until 2 May 1962-1 January 1964 (Townsend 1968) no general survey of the avifauna of San Nicolas Island was attempted." Lynch and Johnson discarded all six apparent cases of turnover suggested by comparison of these two publications and concluded that apparent natural turnover between 1897 and 1962-4 was zero. In fact, the results of one general survey based on three visits by two observers totalling 35 days in 1945 were published in this journal (Rett 1947). Another general survey, by L. Miller in 1938, is described in an unpublished manuscript by Miller in the UCLA library. San Nicolas has the best documented and one of the two highest turnover rates of any Channel Island (12 cases of turnover since 1963 alone). Lynch's and Johnson's erroneous conclusion of zero turnover partly reflects the inevitable underestimate that the in-and-out effect causes with widely spaced survey years, but also reflects more specific errors. Thus, "The Bald Eagle and Osprey, now extinct on the island, were present and possibly resident but good evidence for breeding is lacking" (Lynch and John-

son 1974: 380, col. 1). In fact, an Osprey egg was taken on San Nicolas in 1901 by B. Trask and is in the MVZ collection; a set of three eggs was taken there by C. B. Linton on 15 April 1909 (WFVZ); and Willett (1912, 1933) recorded it as having bred commonly. Rett (1947) and others (egg set in WFVZ) found eagles nesting. "Two species (meadowlark and [Brewer's] blackbird) are native colonists from the mainland that well may have arrived to breed in direct response to habitat alteration by man and his livestock" (Lynch and Johnson 1974: 380, col. 2). As discussed on our p. 533, Western Meadowlarks colonized some time between 1940 and 1945, while Brewer's Blackbirds did not colonize successfully and disappeared after breeding in 1962 and 1963. In 1897 man and his livestock had already been on San Nicolas for at least half a century and had converted most of the island into typical habitat for these two bird species. It is implausible that removal of the livestock in the 1930's was the cause of the colonizations, because on all seven other Channel Islands during this entire period both meadowlarks and livestock coexisted abundantly; and the meadowlark still coexists abundantly with livestock today on the four islands that continue to support livestock. Lynch's and Johnson's claim (1974: 380, col. 2) that Townsend noted no evidence of breeding in the Burrowing Owl and that his observations of the easily identified White-crowned Sparrow require confirmation contradicts Townsend (1968, amplified by personal communication).

(7) Regarding Diamond's study of the New Guinea satellite island of Karkar in 1969 for comparison with Meek's 1914 study, Lynch and Johnson (1974: 381-3) suggested that Diamond could "easily" have overlooked the five apparently extinct species (two rails and three pigeons), and that all 11 of the apparent 1969 immigrants might "quite possibly" have been present in 1914 despite Meek's failure to obtain them. These assessments should surprise workers familiar with the species involved and with field methods in the New Guinea region. On Karkar, as elsewhere in the New Guinea region, many resident people are walking encyclopedias of natural history with detailed knowledge of virtually all resident bird species and of many rare stragglers (Mayr 1932, Gilliard and LeCroy 1961 and many other papers, Diamond 1966 and 1972, Bulmer 1974 and many other papers); their help was used extensively by Diamond's party (consisting of Diamond plus four New Guinea residents and six Karkar residents). The pigeons found by Meek but not by Diamond (Grey Pigeon *Ducula pistrinaria*, Piñon Imperial Pigeon *Ducula pinon*, Nicobar Pigeon *Caloenas nicobarica*) are three of the best known and most conspicuous common species of the New Guinea region. The loud calls of the former two species carry for a mile or more. The two rails found by Meek but not by Diamond are, of course, much shyer but are distinctive species well-known to natives elsewhere and are sometimes common. Karkar natives stated that these two rails were absent but correctly predicted that Diamond would instead find the equally shy rail *Amauornis olivaceus*, a new immigrant, common on Karkar. While a few of the 11 apparent immigrants could have been overlooked by Meek, this is unlikely for such conspicuous, common, and easily collected species as Willie Wagtail (*Rhipidura leucophrys*), Cicada Bird (*Coracina tenuirostris*), and Brahminy Kite (*Haliastur indus*). For some of these immigrants, Karkar residents were able to give details of when and where the species had first appeared.

RECONSTRUCTION OF COLONIZATION BY ENDEMIC RACES THOUSANDS OF YEARS AGO

Lynch and Johnson (1973) claimed that the number of endemic bird subspecies occurring on the Channel Islands argues against high turnover rates. Even if turnover of these endemic races was in fact slow, this would not indicate slow turnover of the avifauna as a whole, since turnover rates vary conspicuously among species. In addition, inter-island movement of all but two of the 13 species with endemic subspecies on the Channel Islands, and of 9 of the 18 endemic subspecies themselves, has been detected in this century, in most cases even within the past decade. Five of these endemic subspecies (*Selasphorus sasin sedentarius*, *Eremophila alpestris insularis*, *Lanius ludovicianus anthonyi*, *Vermivora celata sordida*, and *Aimophila ruficeps obscura*) have established new breeding populations on previously unoccupied islands. Johnson (1972) attempted to use present distributional patterns of the endemic subspecies to reconstruct their ages (in geological time) and island-to-island colonization routes. For instance, he suggested that the Rufous-crowned Sparrow first colonized Anacapa in the Xerothermic or post-Xerothermic period after the end of the Pleistocene, spread from there to Santa Cruz, then died out on Anacapa (Johnson 1972: 301, 310); and that the Western Flycatcher, Horned Lark, Orange-crowned Warbler, and Allen's Hummingbird first colonized the northern islands in the cool-moist period between the end of the Pleistocene and beginning of the Xerothermic, the former two species possibly arriving before the latter two, and spread fairly quickly thereafter to the southern islands (Johnson 1972: 301, 309, 312). In fact, on-going turnover and inter-island movements of these and other endemic bird subspecies of the Channel Islands have probably distorted their original distributions completely beyond recognition and obliterated all but their most recent histories. These movements make attempted reconstructions of their island distributions thousands of years ago too speculative to be useful.

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