TURNOVER AND EQUILIBRIA IN INSULAR AVIFAUNAS, WITH SPECIAL REFERENCE TO THE CALIFORNIA CHANNEL ISLANDS

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According to current biogeographical theory, the number of species comprising an insular biota is the result of a dynamic interaction between extinction and immigration rates. These rates, in turn, are thought to depend primarily on island size and distance from sources of potential colonists (MacArthur and Wilson 1963, 1967). This equilibrium model has been tested in a number of ways, including studies of recolonization of Krakatau, an island whose entire biota was destroyed by a natural catastrophe (MacArthur and Wilson 1967, after Dammerman 1948; Docters van Leeuwen 1936), tallies of the species of terrestrial arthropods present on tiny mangrove islands before and after intentional defaunation (Simberloff 1969; Simberloff and Wilson 1969, 1970; Wilson and Simberloff 1969), and through comparisons of the results of repeated surveys of insular avifaunas (Diamond 1969, 1971; Hunt and Hunt 1974; Terborgh and Faaborg 1973).

It is understandable that ornithology should play an important role in the maturation of this body of theory, as it has in other areas of evolutionary biology. Compared with most other kinds of organisms, birds are relatively easy to observe and are well known taxonomically and biologically. Moreover, birds have been studied over a sufficient period in some regions so that it is possible to compare recent surveys with others going back 50 years or more.

Unfortunately, the gathering and interpretation of avifaunal data present more problems than are generally realized and, unless these difficulties are overcome, a proper test of the MacArthur-Wilson theory that uses ornithological information is not possible. The goals of the present paper are to describe some of the problems inherent in studies of turnover in insular avifaunas, to develop a series of criteria for the evaluation of avifaunal data, and to apply these criteria to examples of studies of avifaunal turnover described in the recent literature.

EQUILIBRIUM THEORY AND AVIFAUNAL TURNOVER

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. The validity of the first of these predictions has been examined in numerous studies (e.g., Hamilton et al. 1964; Hamilton and Armstrong 1965; Hamilton and Rubinoff 1967; Wilson 1961; Power 1972; Vuilleumier 1970, 1973; Brown 1971; Johnson and Raven 1973; Harris 1973), most of which report a positive correlation between species number and island size and/or proximity to a source of colonists. While the examination of the species-area relationship is not of direct concern in the present paper, it should be mentioned that after a careful analysis of patterns of intercorrelation, Power (1972) found that for the California Channel Islands avifaunal complexity is tied to aspects of ecological diversity rather than to island size or isolation per se. Similar results were reported earlier by Koopman (1958) in a study of the diversity of bats on islands off the coast of South America and by Watson (1964) in a study of bird species diversity on Aegean islands. MacArthur and Wilson (1967) noted that ecological factors correlated with area, rather than area itself, probably control species diversity, but some other workers have tended to emphasize the apparent importance of area and distance to the exclusion of more immediate influences.

In this paper we direct attention to the second aspect of the equilibrium theory, the question of faunal turnover. If this part of the theory is relevant to an island avifauna, then repeated surveys should reveal all of the following: (a) there should be a measurable rate of faunal turnover (as opposed to a static situation); (b) the number of species present should remain approximately constant (i.e., there should not be an excess of extinctions over colonizations, or vice versa); and (c)

turnover should reflect the stochastic nature of an equilibrium condition (i.e., the turnover should not be attributable to some systematic bias such as ecological succession, human disturbance of habitats, introduction of exotic species, etc.). Verification of (a) and (b) requires a reliable and relatively complete baseline survey of breeding species as well as an adequate resurvey of the insular fauna. Evaluation of (c) requires additional knowledge of the history of the island and its fauna.

DEFINITIONS OF COLONIZATION AND EXTINCTION

At the outset, it is necessary to adopt consistent definitions of colonization and extinction. MacArthur and Wilson (1967:186) defined these terms as follows: "*Colonization.* The relatively lengthy persistence of an immigrant species on an island, especially where breeding and population increase are accomplished." "*Extinction.* The total disappearance of a species from an island (does not preclude recolonization)." For highly mobile, behaviorally complex organisms such as birds, we believe it necessary to modify these definitions slightly in order to emphasize the overriding importance of breeding activity as a criterion for colonization and extinction. For organisms which are capable of repeated long-distance movements to and from a permanent or temporary living site, and which may leave and return on the basis of a daily, seasonal, or other temporal cycle, the only unambiguous assay by which colonization can be distinguished reliably from more transient modes of visitation is the occurrence of reproductive activity. Simberloff and Wilson (1969) recognized this basic difference between mobile organisms (e.g., birds, butterflies, many Dipterans, many Hymenopterans, etc.) and animals which reach islands by more passive means. These authors did not count animals of the former category (e.g., the wasp *Polistes*) as valid colonists of mangrove islands unless definite evidence of breeding was found.

One consistent alternative is to count *all* visitants as immigrants (which also entails counting each one as an extinction when it leaves the island), a convention, which, as MacArthur and Wilson noted (1967:64), "magnifies 'extinction' beyond what most persons would accept." There are other problems with the latter convention when applied to birds. First, because the number of migrant, visitant, and stray species tends to be so much greater than the number of species which actually colonize an island (see discussion in the following section), an apparent balance between

"colonization" and "extinction" results from the unsurprising fact that transient species are, in fact, transient, i.e., that they both arrive ("colonize") and leave (become "extinct"). Such comings and goings may be of considerable interest in other contexts, but they probably have little direct bearing on the equilibrium size of an insular avifauna. The second problem with the use of simple presence as a criterion for colonization is that it is largely nonoperational. Without a major commitment of time and resources, one cannot monitor the arrivals and departures of all birds even on a relatively small island.

Intermediate definitions of colonization and extinction that require some degree of persistence or "potential" of breeding, but not necessarily breeding activity, are possible (see Simberloff 1969; MacArthur and Wilson 1967: 64), but these suffer from the fact that there is no operational, unambiguous criterion for distinguishing between colonization and mere arrival of casuals and migrants. Keeping the above considerations in mind, we have modified slightly MacArthur and Wilson's definitions: *Colonization.* The persistence of an immigrant species on an island as a breeding population through at least one reproductive cycle. *Extinction.* The total disappearance from an island, for at least one reproductive cycle, of a species which had formerly bred there (does not preclude recolonization).

By emphasizing the criterion of reproductive activity we do not imply that migrant birds, or other nonbreeders, are necessarily unimportant influences on the composition and turnover of insular avifaunas. Indeed, competition with nonbreeding migrant species, which frequently outnumber "native" forms in local situations, may have profound effects on all the species involved. The point is that any such influences cannot be evaluated from the kinds of data which have been used to compute avifaunal turnover rates. The arbitrary inclusion of some nonbreeding species as "residents" while others are dismissed as migrants or casual visitants only serves to confuse matters.

KINDS OF AVIFAUNAL TURNOVER

The question of possible habitat change assumes crucial importance in attempts at interpreting natural rates of turnover. Often it has been assumed tacitly in discussions of equilibrium theory that variation in habitat is either nonexistent, or unimportant, or at least is unassessable. Instead, the importance of area and distance effects are stressed. In recent years, however, concern with the rela-

tive role of habitat versus area-distance effects has become prominent in the literature (see, for example, Lack 1971, 1973 *contra* Terborgh 1973).

We accept as an axiom of biogeography that all faunas are dynamic to some extent, with temporal fluctuations occurring in composition by species and in density within species. The time scale of such fluctuations may vary from a few months or less to many thousands of years. At one extreme, one can envision changes in the composition of an avifauna related to the slow shift in the habitats of an area in response to climatic change. In such a situation a series of climax communities might occupy a given site, each community giving way to the next over a period of hundreds or thousands of years. In California, such a sequence might involve a gradual shift from grassland, with a maximum of 55 breeding species of birds (Miller 1951a), through chaparral (43 species), to oak woodland (63 species) over a span of several hundred years, perhaps in response to long-term changes in rainfall pattern. As shown in this example, the same equilibrial number of species would not be expected for each plant formation in view of their differing carrying capacities (differing potentials to support diversity). Such long-term natural faunal replacement in response to climax habitat change at one site may be termed *paleoturnover*. The fossil record abundantly documents our assumption that such changes have happened routinely in the past.

Such community turnover in response to gradual climatic trends can be contrasted with shorter-term changes in species composition and abundance. Different avifaunas will occupy successive seral stages of vegetation which have developed in response to local modification of plant communities within the same climatic regime. These short-term changes, such as might be observed in the fauna inhabiting the various stages of vegetation returning to a forest climax after burning, may be termed *successional turnover*. This kind of turnover could result either from natural causes (lightning fire, explosion of a volcano) or from direct or indirect human activity. Examples of human activities that provide transitory habitats or seral stages of vegetation suitable for species not previously present include agriculture, installation of water impoundments, and modification or destruction of vegetation by cutting and grazing. Human influence on turnover rates may also occur through the direct or indirect introduction of non-native species and the extirpation

of native species by pesticides and other poisons, predation by domestic and feral animals, and shooting.

Finally, we can define *equilibrium turnover* as the change in species composition which occurs in a stable ecologic setting, independent of and uninfluenced by human activities.

Thus, faunal turnover is seen to be a complex phenomenon resulting from a multiplicity of causes and amenable to interpretation beyond the standard discussions of the current literature.

PROOF OF TURNOVER

What kinds of data are necessary to prove that faunal turnover of *any* sort has occurred on an island? For birds, detection of turnover requires a thorough baseline survey, taken during a restricted time period and documented by proper evidence of residence of each species, which can be compared with a similar but later survey of the same island. The primary criterion for residence on an island by a bird species is the occurrence of at least one *breeding* pair. 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. As an example, we cite below data for the Farallon Islands off the coast of central California. Coastal islands are notorious for their accumulation, at all seasons, of a staggering variety of migrant, stray, and sexually inadequate laggard birds. In the absence of specific information on reproductive activity, it is therefore unwarranted to assume tacitly that a bird species, even if observed in the breeding season, is resident. Ideally, documentation of breeding should consist of actual nesting records or observation of recently fledged young birds attended by parents, preferably with voucher specimens. The observation of a singing male evidently defending a territory is a less reliable indicator of breeding activity, because such a male may be unmated; indeed, in insular settings, there may be no potential mate that is accessible. Here again, data on gonad condition are important when one must decide on the likelihood of breeding versus migrant or casual status.

Extinction, the disappearance of a formerly *breeding* population, requires proof that the species was indeed breeding at one time *and* strong evidence of absence during the later survey. The absence of rare and inconspicuous species may be extremely difficult to establish in a short time, especially if the island being explored is large. Certain raptors

TABLE 1. Nonbreeding land birds banded on the Farallon Islands, California.[a]

Year	Total species				Total individuals			
	May	June	July	Aug.	May	June	July	Aug.
1968	40	18	11	31	328	24	13	117
1969	46	50	11	17	637	307	13	68
1970	49	32	6	33	445	84	6	215
1971	44	17	2	8	630	30	2	13
1972	32	26	10	34	185	59	18	80
Mean	42	29	8	25	445	101	10.4	98.6

[a] Unpublished data of David G. Ainley, T. James Lewis, and Henry Robert, Point Reyes Bird Observatory, Bolinas, California.

are obviously a problem in this regard, but other birds, including passerines, may be highly localized and difficult to find in a brief survey.

Vagrant and migrant land birds on the Farallon Islands, California. As support for our thesis that the coastal islands of California are visited routinely during the summer months by large numbers of nonbreeding land birds, we summarize recent banding data from the tiny (0.16 square mile) Southeast Farallon Island, located 20 miles off the coast of the central part of the state (table 1). Because the Rock Wren (*Salpinctes obsoletus*) is the only species of land bird known to breed at present on the island (D. G. Ainley and T. J. Lewis, unpubl. data), records of it can be excluded. All the totals in table 1 involve migrants and other transient individuals. The figures are minimal estimates of numbers actually present because not all birds seen are caught and some are released without banding. These data significantly clarify several poorly understood aspects of the dynamics and composition of insular bird populations.

First, it is apparent that vagrants, late "spring" transients, and/or early "autumn" transients occur regularly. At least a few individuals of several species were banded in every summer month for each of the 5 years over which data were kept. Thus, there is no period of the summer when it can be assumed safely that a bird is an established resident, based on date of occurrence alone. Second, the carefully gathered banding records show conclusively that surprisingly large numbers of species and of individuals are involved (because each bird in table 1 was marked, the possibility of repeated tallies of the same individual was excluded). Average numbers varied from a minimum of eight birds of eight species in July to 445 individuals of 42 species in May. Occasionally, the number of summer visitants was spectacular, as in June 1969 when 307 individuals of 50 species of land birds were banded, none of them species that have ever bred on these islands.

Finally, because these bleak islands completely lack appropriate breeding habitat for virtually all of the recorded land bird species, it is evident that the islands attract these migrants and strays primarily as resting stops or refuges, and not because the skimpy traces of vegetation there offered likelihood, or even the possibility, of successful breeding. In other words, even the smallest islands along the coast *actively accumulate* migrant and vagrant land birds during the late spring and also in the summer months when one assumes that only breeding species ordinarily are present. Certainly, larger islands would attract even greater numbers of land birds.

These data support our contention that the presence of nonbreeding land birds on continental islands is the rule rather than the exception, and that the only way to analyze properly insular avifaunal records in studies of turnover is to eliminate such records of vagrants and migrants from consideration and to concentrate solely on species of proven breeding status.

THE RELEVANCE OF REAL TURNOVER

Once avifaunal data have been screened to eliminate spurious instances of immigration and extinction attributable to inadequate information (i.e., "pseudoturnover"), one still faces the problem of interpreting the significance of any turnover which actually has occurred. As was noted earlier, several disparate factors may contribute to observed changes in resident status, and it is important to distinguish between turnover related to human activities and/or successional changes in insular habitats on the one hand, and that which could be attributed to a steady-state equilibrium condition on the other. At least for continental islands, the abundant occurrence of potentially breeding species that continually pass through island habitats can be envisioned as evidence for persistent "testing" of the insular setting for suitability. Some of these species are able to capitalize very rapidly on favorable changes in habitat that might occur as the result of fire succession, agricultural

activity, introduction (or removal) of grazing mammals, or other causes. The number and identity of such opportunistically invading (or disappearing) species may not be controlled primarily by area-distance effects, but by the timing, extent, and nature of changes which may occur in the insular habitats. Use of an equilibrium model in such situations is inappropriate. Application of the latter kind of model should be restricted to instances where faunal turnover is plausibly attributable to stochastic processes (i.e., random colonizations and extinctions). Interpretation of faunal change is especially difficult if both equilibrium and nonequilibrium (successional) turnover are involved, as apparently has been the case for the repopulation of Krakatau by plants and animals following the devastation of that island by a volcanic eruption (see MacArthur and Wilson 1967).

Studies such as those of Diamond (1969, 1971) and Terborgh and Faaborg (1973) concern equilibrium turnover as that term is defined in this paper. These authors report relatively high rates of species turnover, and while instances of human influence upon turnover are mentioned in passing, the overall importance of human-related changes is minimized (for example, see Diamond 1969:60, 1971:2743). We therefore feel justified in inquiring whether the available data support the conclusions reached in these studies.

Avifaunal turnover rates on the California Channel Islands will be considered in some detail. These islands have been the object of considerable biological interest in recent years and both of the present authors have had some field experience on several of them. More importantly, the Channel Islands are of particular interest in the present context because their avifauna has been studied by Diamond (1969) specifically in relation to the MacArthur-Wilson equilibrium model. This analysis, which has been cited in all subsequent turnover studies, also has served as a basis for comparison with turnover rates in other geographic regions (Diamond 1971; Terborgh and Faaborg 1973).

Diamond's studies (1969, 1971) will be examined in the light of a set of explicit criteria that are based upon the topics discussed earlier and are applicable to any study of turnover rates which depend on repeated surveys of insular avifaunas.

CRITERIA USED TO EVALUATE POSSIBLE EXTINCTIONS AND IMMIGRATION

Extinction. If the apparent disappearance of a bird species between an earlier survey and a later survey is to constitute a valid equilibrium extinction, *all* of the following conditions must be satisfied:

E1. The resident status of the species at the time of the earlier survey must be reasonably certain. In the absence of direct evidence of former breeding status, such factors as known presence of numbers of individuals during the appropriate breeding season, and the breeding distribution of the form on nearby islands or on the mainland may be considered, but such information can provide, at best, only weak supportive arguments. Simple sight records of wide-ranging forms without data on reproductive condition do not constitute valid evidence of breeding status.

E2. There must be convincing evidence that the species truly was absent from the island at the time of the later survey. In the case of conspicuous diurnal raptors or of normally obvious and well-dispersed passerines, apparent absence during the breeding season is acceptable evidence, although even in these examples error is possible if the island is large. Simple failure, over the course of a few days, to observe species which are known to be inconspicuous, rare, nocturnal, and/or hole-roosting does not constitute presumptive evidence of extinction, especially when a large island is involved, or when a small island was visited briefly and/or at the wrong season.

E3. Human influence must not have played a significant role in the demise of the species. This criterion excludes from the category of natural extinctions those extirpations caused by pesticides, shooting, and habitat changes related to the activities of man or his associated animals.

E4. Natural successional changes in habitat must not have had an important influence on the extinction.

Immigration. The valid addition of a bird species through equilibrium turnover to the fauna of an island requires that *all* the following criteria be satisfied:

I1. It must be reasonably certain that the species actually was absent at the time of the earlier survey. The same comments made under E2 apply here.

I2. There must be specific evidence that a breeding population was present at the time of the later survey (see E1).

I3. The species must have been an integral part of the native species pool available on the adjacent mainland in earlier years. This criterion would exclude colonizations by exotic species recently introduced to the mainland source area.

TABLE 2. Avifaunal turnover on the Channel Islands (from Diamond 1969:59).

	Area A	Distance B	1917 species C	1968 species D	Extinctions E	Additions F	Introductions G	Immigrations H	Turnover I
Los Coronados	1.0	8	11	11	4	4	0	4	36
San Nicolas	22	61	11	11	6	6	2	4	50
San Clemente	56	49	28	24	9	5	1	4	25
Santa Catalina	75	20	30	34	6	10	1	9	24
Santa Barbara	1.0	38	10	6	7	3	0	3	62
San Miguel	14	26	11	15	4	8	0	8	46
Santa Rosa	84	27	14	25	1	12	1	11	32
Santa Cruz	96	19	36	37	6	7	1	6	17
Anacapa	1.1	13	15	14	5	4	0	4	31

For each island, column A gives the area in square miles; B, the distance in miles from the nearest point on the mainland; C, the number of species of land and freshwater birds breeding in 1917; D, the number of breeding species in 1968; E, the number of species that were breeding in 1917 but not in 1968 and hence must have gone extinct in the interim; F, the number of species breeding in 1968 but not in 1917 ("additions"); G, the number of species present in 1968 that had been successfully introduced by man between 1917 and 1968 (all of these are game birds: California quail, Gambel's quail, pheasant, or chukar); H, the number of species present in 1968 but not in 1917 that had immigrated under their own power between 1917 and 1968, calculated as F minus G; and I, the turnover rate expressed in percent of the species pool per 51 years, calculated as $100(E + H)/(C + D - G)$.

I4. Human activity (e.g., direct introduction, elimination of predators, modification of the habitat) must not have played an important role in the establishment of a breeding population of the species.

I5. The species must require and occupy a habitat which was available at the time of the earlier survey.

THE CALIFORNIA CHANNEL ISLANDS

Diamond (1969) reviewed distributional records of land birds for the Channel Islands (including Los Coronados) off the coast of southern California, as summarized by Howell (1917) and as compared with records obtained by Diamond and his assistants in 1967–68, and concluded that: (1) the total number of bird species resident on each island has tended to remain fairly constant, and therefore at equilibrium, in the 51 years which elapsed between the two surveys; (2) the species composition of the avifauna has changed markedly on most islands, indicating unexpectedly high turnover rates (17–62%) of breeding bird species; and (3) turnover rates are independent of island size or distance to the mainland, but are correlated inversely with the total number of bird species present. Stability in species *numbers* in the face of dramatic instability in species *composition* supports the notion of a dynamic equilibrium process, and Diamond's paper has been cited as an important confirmation of the theory of insular species equilibrium (MacArthur 1971, 1972).

Detailed information on the Channel Islands and their birds can be obtained from Howell (1917), Philbrick (1967), Thorne (1969), Johnson (1972), and Power (1971, 1972). Table 2 (from Diamond 1969) summarizes several aspects of the geography and reported avifaunal turnover rates for the nine islands.

Because the majority of records and identity of individual bird species which support Diamond's turnover figures in table 2 were not published, his figures are impossible to interpret properly. Some additional identifications are provided in a later paper (Diamond 1971), but we are unable to identify here the remaining unnamed species. Therefore, where possible, we have sought avifaunal records for certain islands from the primary literature in order to reanalyze turnover rates.

THE ADEQUACY OF THE AVAILABLE DATA BASE

The status of species supposedly breeding or absent in 1917. Diamond's determinations of which species were present as breeding populations on the various islands were based upon records included in Howell (1917). A potentially important criticism of this assumption of a 1917 "baseline" is that Howell's paper is a summation of *all* records ever obtained up to that time and is therefore not directly comparable to the censuses undertaken by Diamond in 1967–68. Observations made as early as the 1860s (for example, Cooper 1868, 1870) are included in Howell's compilation and there are numerous references to observations made in the period of 1880–1900. The assumption that all species listed as resident by Howell were actually present and breeding in 1917 is perhaps reasonable if one assumes very low turnover rates, but seems questionable if, as Diamond maintains, rapid turnover rates are in fact the rule. The result of including all records up to 1917 is to overestimate the turnover rate by some unknown fraction. We will ignore this source of error in the following analysis. However, it is worth pointing out that in this instance, as in several others, inat-

tention to detail concerning source materials
leads to inflation of the apparent turnover
rates.

A more important drawback of Howell's list
is that it is so obviously incomplete for some
of the islands. Diamond (1969:58) mistakenly
claimed that "Howell himself spent periods of
several weeks on each island." Actually,
Howell (1917:5) stated, "I regret that I have
been unable to spend more time myself in
field work—some weeks, at least, on each
island. There seems no prospect of this in the
near future, and further delay of publication
for this reason seems unwise. As a matter of
fact, *there has been comparatively little work
done upon these islands by anybody. . .*"
(italics ours). Thus, Howell's summary is not
the result of an extensive and systematic pro-
gram of field work in the islands. Instead, like
many faunal compilations of that period, it is
dependent to an undesirable (albeit under-
standable) degree upon second-hand and
anecdotal data. Moreover, the information
available to Howell was especially incomplete
for certain islands, notably Santa Rosa and San
Miguel, because of problems in obtaining per-
mission to work there. Diamond acknowl-
edges this bias in Howell's list and even identi-
fies the islands which were poorly known;
surprisingly, he proceeds anyway to include
the incomplete data for these islands in his
calculations. The kind of error introduced by
such uncritical use of fragmental faunal data
can be appreciated when one compares the
results of the first reasonably extensive survey
of Santa Rosa (Pemberton 1928) with
Howell's list. Pemberton listed nine species of
resident land birds (including several for
which he obtained definite nesting records)
which Howell did not record in his 1917 paper.
The fact that Diamond (1969:59) listed 11
species as having *immigrated* to Santa Rosa
since 1917, because they were present in 1968
but "absent" in 1917, must be interpreted with
this latter observation in mind.

While the Santa Rosa example is perhaps
the most obvious instance where turnover rates
have been artificially inflated by the use of
an incomplete baseline survey, problems exist
even for islands considered reasonably well
explored at the time of Howell's summary.
Especially where the species in question are
uncommon, relatively secretive, and/or wide-
ranging as nonbreeders [for example, the vari-
ous owls, or the Barn Swallow (*Hirundo
rustica*)], sight records or lack thereof may
have little or no significance with regard to
breeding status. As will be shown below,
examples of supposed extinction which are

based on such observations comprise an ap-
preciable fraction of Diamond's turnover rates.
We know of but a single instance in which
a comparatively adequate early survey of one
of the Channel Islands can be compared with
a detailed recent study of the same island.
This is the pair of studies of the avifauna of
San Nicolas by Grinnell (1897) and Townsend
(1968). Importantly, when the records from
each survey are evaluated critically the re-
sultant avifaunal turnover rate is *zero* (see
below).

We conclude that Howell's summary is by
no means an adequate survey of the land birds
breeding on the Channel Islands as of 1917.
Accordingly, caution is required in assessing
the probable status of the insular avifaunas
in 1917. If individual records are appraised
critically, then the Howell work is quite useful.
In the absence of such concern for details,
Howell's paper provides an undependable
basis for determining which species of birds
actually were resident on or absent from the
various Channel Islands in the early years of
the present century.

*The status of species reported as breeding
or absent in 1967–68.* Diamond and his as-
sistants did no scientific collecting in 1967–
68. Thus, information on gonad condition of
the birds reported to be resident is lacking
and the possibility of misidentification of at
least a few species cannot be dismissed. Al-
though there is no objective way to deal
with the problem of species identification in
the absence of specimens, one is justified in
questioning judgments on breeding status of
an unidentified group of species when no
supportive data were published or provided
otherwise.

MODES OF EXTINCTION ON THE
CALIFORNIA CHANNEL ISLANDS

Diamond (1969) listed 48 bird populations as
having become extinct on the Channel Islands
between 1917 and 1968. Unfortunately, many
of these supposed extinctions are not identi-
fied, but by reference to later papers (Dia-
mond 1971; Hunt and Hunt 1974) 41 of the
48 extinctions can be assigned to species and
island. The identifiable extinctions fall into
several modes.

Human activities. Eighteen extinctions in-
volve the Bald Eagle (*Haliaeetus leuco-
cephalus*) (8), Peregrine Falcon (*Falco
peregrinus*) (7), and Osprey (*Pandion hali-
aetus*) (3). These three raptors have disap-
peared from all the islands where they for-
merly bred (Diamond 1969:60). As Diamond
himself noted, these disappearances occurred

over the same period of time when the three species declined virtually to extinction on the mainland of central and southern California. The "turnover" in these species has been strictly unidirectional, hardly what one would expect of an equilibrium process. In fact, the precipitous decline of these large birds of prey is clearly related to the adverse effects of human activities. These activities have included intense egg-collecting, removal of nestlings for falconry, shooting of adults, intentional poisoning, and introduction of pesticides into the food web. The disappearance of the Bald Eagle, Peregrine Falcon, and Osprey account for 44% of the identifiable extinctions counted by Diamond (38% of the total extinctions).

Of the remaining 23 identifiable extinctions, three involve the Common Raven (*Corvus corax*), a species which formerly bred on all of the Channel Islands according to Howell (1917). Here, too, "turnover" has been a one-way process, and again human influences of the sort just mentioned are strongly implicated as contributing to this series of extinctions. Another relatively clear-cut instance of human interference is the extinction of the endemic race of the Song Sparrow (*Melospiza melodia graminea*) on Santa Barbara Island. As has been noted by several authors (Diamond 1969; Philbrick 1967; Hunt and Hunt 1974), this tiny (1 square mile) island has been devastated in recent years, both by fire and the depredations of introduced rabbits and cats. Unsurprisingly, the formerly abundant Song Sparrow responded to the elimination of its breeding habitat by declining to extinction. Hunt and Hunt (1974) note that the House Finch (*Carpodacus mexicanus*) has suffered a similar fate on Santa Barbara Island, although there appears to be some question as to whether a few individuals have persisted. The Costa's Hummingbird (*Calypte costae*), another former breeding resident of the island, also may be a casualty of habitat destruction; although from the remarks of Hunt and Hunt (1974), individuals of this species still may be present, perhaps as vagrants, at very low densities (see below).

Disregarding the last two cases because of uncertainties in the available data, there are at least 22 disappearances of bird populations which can reasonably be attributed to human interference. These comprise 54% of the identifiable extinctions claimed by Diamond (45% of the total extinctions).

Pseudoturnover. A number of extinctions listed by Diamond involve species which have not been shown to breed and may never have bred on the islands in question. For example, Diamond claims that the Lark Sparrow (*Chondestes grammacus*) became extinct on Santa Cruz Island sometime after 1917. In fact, the only basis for the supposed former breeding status of the species is Linton's (1908) December sight record of a probable winter vagrant. Similarly, Diamond lists the Red-shafted Flicker (*Colaptes cafer*) as having gone extinct on San Clemente subsequent to Howell's survey. Actually, Howell (1917) did not record the species from San Clemente Island. A check of the earlier literature reveals a record of two specimens collected by Linton (1908). However, these were taken during the height of the fall migratory period, and cannot be construed as evidence of breeding status. Grinnell and Miller (1944:228) concluded that there was no indication of nesting by the flicker on San Clemente.

Another example of pseudoturnover is provided by the supposed extinction of the Lawrence's Goldfinch (*Spinus lawrencei*) on Santa Cruz and Santa Catalina islands. This species has never been shown to breed on any of the Channel Islands, and Howell's only records are for sightings during April and May, a time when migrants and stragglers would be passing through the islands. The inclusion of the Anna's Hummingbird (*Calypte anna*) 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. 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.

Four presumed extinctions involve the Burrowing Owl (*Speotyto cunicularia*), a notoriously wide-ranging visitant and vagrant. Although this species may breed in the islands,

to our knowledge it has never been proved to nest on any of the California Islands from which it has supposedly disappeared. As in the last example, the problem of evaluating the status of the Burrowing Owl is compounded by the fact that the species may easily be overlooked in a short survey, particularly on a fairly large island. Similarly, the "extinction" of the Long-eared Owl (*Asio otus*) on Catalina (Diamond 1971) can reasonably be attributed to failure to record a species which can be very difficult to find when it is roosting. Put simply, absence of records of owls does not prove absence of the birds and verification of their presence is not necessarily also proof of their residence.

Even passerines may be sufficiently rare and localized so that absence is difficult to establish on the basis of a short survey. The Black Phoebe (*Sayornis nigricans*) is such a species. Diamond lists it as having become extinct on San Clemente after 1917. The species was certainly resident prior to 1917 (Linton 1908), but was always considered rare and thought to be confined to a small area on the northwest coast of the island (Howell 1917). Grinnell (1897) collected birds on San Clemente for 17 days during the breeding season, but he worked at the southern end of the island and did not observe any Black Phoebes there. That Diamond did not see the species during his visit to the island is unacceptable evidence of its present absence from San Clemente unless the entire coastline of this large island was carefully examined.

Possible examples of equilibrium turnover. The instances of human-related turnover and pseudoturnover together appear to account for 33 of 41 (80%) identifiable extinctions cited by Diamond. The question remaining is whether any of the seven remaining extinctions are well enough documented to provide strong evidence for equilibrium turnover.

Two of the extinctions involve the Red-breasted Nuthatch (*Sitta canadensis*) and Cooper's Hawk (*Accipiter cooperii*) on Santa Cruz Island. 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 and both are widespread as migrants or vagrants. The Red-breasted Nuthatch, for example, has appeared in large numbers on the Farallon Islands.

The Common Bushtit (*Psaltriparus minimus plumbeus*), supposedly extinct on Catalina Island, was never shown to breed there, and the early sight records by Willett (*fide* Howell 1917) may well have involved a vagrant group which was blown to Catalina from the main-

land. No other observers have ever reported the Bushtit on Catalina. Diamond claims that the Allen's Hummingbird (*Selasphorus sasin*) and Barn Swallow have become extinct on Los Coronados. While this is possible, neither has ever been shown to breed there, and both are abundant and widespread as migrants.

Only two identifiable natural extinctions involve species that were definitely known to have bred previously and can reasonably be inferred to have been absent at the time of Diamond's survey. One is the Costa's Hummingbird, which is supposed to have disappeared from Santa Barbara Island. However, as noted earlier, human activities have so altered the vegetation of that island that any extinctions should be viewed with suspicion. Moreover, Diamond (*fide* Hunt and Hunt 1974) and Hunt and Hunt (1974) observed unidentified hummingbirds on the island, so that the Costa's Hummingbird may in fact still be present as a rare resident.

The single remaining extinction is the Red-tailed Hawk (*Buteo jamaicensis*) on San Clemente. The species is definitely known to have bred on the island (Howell 1917), and Diamond is unlikely to have overlooked this conspicuous raptor at the time of his census.

In summary, we conclude that the great majority of extinctions reported by Diamond to have occurred on the California Channel Islands are attributable either to human interference or to faulty interpretation of faunal data (pseudoturnover). While a few "natural" extinctions *may* have occurred, we can find only a single reasonably well-documented example out of 41 specified extinctions.

IMMIGRATION OF SPECIES TO THE CHANNEL ISLANDS

Diamond's figures for immigrations are difficult to evaluate because so few of the supposed colonists are identified. It should be noted, however, that 19 of 41 (46%) of the supposed colonizations are additions to the avifaunas of Santa Rosa and San Miguel, the two islands which were the most poorly known at the time of Howell's survey.

Of the ten supposed colonizations which can be identified, four involve wide-ranging raptors for which nesting records are an absolute necessity if residence is to be inferred (table 3). An additional colonizer is the Common Coot, which is now resident on Santa Catalina on a man-made reservoir (Diamond 1969:60). Three passerine species, Black Phoebe, House Wren (*Troglodytes aedon*), and Chipping Sparrow (*Spizella passerina*), are said to have colonized Los Coronados

TABLE 3. Extinctions and immigrations claimed by Diamond to have occurred on the California Islands between 1917–68. Identifications from Diamond (1969, 1971) and Hunt and Hunt (1974).

Island	Extinctions		Immigrations	
Los Coronados	*Falco peregrinus*	E3	*Falco sparverius*	I2?
	Selasphorus sasin	E1?	*Sayornis nigricans*	I2?
	Hirundo rustica	E1?	*Troglodytes aedon*	I2?
	Corvus corax	E3	*Spizella passerina*	I2?
	(4 + 0 = 4)[a]		(4 + 0 = 4)	
San Nicolas	*Falco sparverius*	E1		
	Haliaeetus leucocephalus	E3		
	Pandion haliaetus	E3		
	Speotyto cunicularia	E1		
	(4 + 2 = 6)		(0 + 4 = 4)	
San Clemente	*Falco peregrinus*	E3		
	Haliaeetus leucocephalus	E3		
	Pandion haliaetus	E3		
	Buteo jamaicensis[b]			
	Speotyto cunicularia	E1,E2		
	Calypte annae	E1		
	Colaptes cafer	E1		
	Sayornis nigricans	E2		
	(8 + 1 = 9)		(0 + 4 = 4)	
Santa Catalina	*Falco peregrinus*	E3	*Fulica americana*	I4
	Haliaeetus leucocephalus	E3	*Melanerpes formicivorus*[b]	
	Pandion haliaetus	E3		
	Asio otus	E2?		
	Psaltriparus minimus	E1		
	Spinus lawrencei	E1		
	(6 + 0 = 6)		(2 + 7 = 9)	
Anacapa	*Falco peregrinus*	E3		
	Haliaeetus leucocephalus	E3		
	Speotyto cunicularia	E1		
	(3 + 2 = 5)		(0 + 4 = 4)	
Santa Barbara	*Falco peregrinus*	E3	*Falco sparverius*	I2
	Haliaeetus leucocephalus	E3	*Tyto alba*	I2?
	Calypte costae	E2,E3	*Speotyto cunicularia*	I2
	Corvus corax	E3		
	Melospiza melodia	E3		
	(5 + 2 = 7)		(3 + 0 = 3)	
San Miguel	*Falco peregrinus*	E3		
	Haliaeetus leucocephalus	E3		
	Speotyto cunicularia	E1		
	Corvus corax	E3		
	(4 + 0 = 4)		(0 + 8 = 8)	
Santa Rosa	*Haliaeetus leucocephalus*	E3		
	(1 + 0 = 1)		(0 + 11 = 11)	
Santa Cruz	*Falco peregrinus*	E3	*Melanerpes formicivorus*[b]	
	Haliaeetus leucocephalus	E3		
	Accipiter cooperi	E1		
	Sitta canadensis	E1		
	Spinus lawrencei	E1		
	Chondestes grammacus	E1		
	(6 + 0 = 6)		(1 + 5 = 6)	
Totals:	41 identified		10 identified	
	7 unidentified		43 unidentified	
	48 "extinctions"		53 "immigrations"	

[a] Figures in parentheses indicate the number of extinctions identified, unidentified, and the total number claimed by Diamond.
[b] Valid extinction or colonization.

since 1917. One of these (House Wren) is not known to breed on any other Channel Island although it is a common transient. Certainly this record requires strong verification in the form of direct breeding evidence if Diamond's interpretation is to be accepted. The other two passerines are known as breeding species on several of the Channel Islands, but more information about their presence on Los Coronados is necessary before they can be tallied as natural immigrants.

The only independently documented equilibrium colonizations of the Channel Islands are the invasions of Santa Catalina and Santa

TABLE 4. Turnover in the avifauna of San Nicolas Island, California.[a]

Extinctions	Immigrations
Haliaeetus leucocephalus E1, E3.[b]	*Phasianus colchicus* I4, I5?
Pandion haliaetus E1, E3.	*Passer domesticus* I3, I4, I5.
	Sturnella neglecta I4, I5?
	Euphagus cyanocephalus I4, I5.

[a] Based on the surveys of Grinnell (1897) and Townsend (1968).
[b] The code following each name refers to criteria by which each instance of extinction and immigration was evaluated. None of the instances listed here provides an acceptable example of equilibrium turnover.

Cruz by the Acorn Woodpecker (*Melanerpes formicivorous*) (summarized by Pitelka 1950; Miller 1951b, 1955). It is unlikely that the species was overlooked by earlier workers, although Pitelka (1950) entertained doubts as to their former absence from Santa Cruz.

INDEPENDENT APPRAISAL OF TURNOVER ON SAN NICOLAS ISLAND

For San Nicolas Island the availability of reliable early and recent surveys, taken independently of Howell (1917) and of Diamond (1969), permits reappraisal of turnover of the resident avifauna (table 4).

Grinnell (1897) was the first ornithologist to survey San Nicolas Island in a comprehensive manner and to publish data based upon specimens and careful field notes. He remarks (p. 9) that San Nicolas "supports a herd of sheep" and that it is "the most barren island of the group." He collected on the island from 19 May to 26 May 1897, and recorded nine species of land birds. From Grinnell's thorough work, we can conclude that three species of birds were definitely resident: Horned Lark (*Eremophila alpestris*), House Finch, and Rock Wren, and that a fourth (Raven, *Corvus corax*) was probably resident. The Bald Eagle and Osprey, now extinct on the island, were present and possibly resident but good evidence for breeding is lacking.

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. Townsend "made observations daily in some areas and weekly in others. The entire island was surveyed at least once monthly." Although Townsend collected no specimens he was cognizant of the importance of breeding data and commented on the nesting activity of several species. The extent and detail of Townsend's records permit them to serve as a survey of the status of the avifauna of San Nicolas Island in 1962–63. He recorded 31 species of land birds, 15 of which were seen during the nonbreeding season for varying periods; these were assumed to be migrants or vagrants. Sixteen species were found during the late spring or summer; for seven of these,

no evidence of breeding was noted [Redtailed Hawk, Mourning Dove (*Zenaida macroura*), Burrowing Owl, Bank Swallow (*Riparia riparia*), Mockingbird (*Mimus polyglottos*), Loggerhead Shrike (*Lanius ludovicianus*), and Song Sparrow]. Records of the White-crowned Sparrow (*Zonotrichia leucophrys*), a species reported to be present in small numbers in all months, and for which it is stated that "Immature birds were observed begging for food, but no nests were found," require confirmation. Unequivocal evidence in the form of specimens with gonads in breeding condition and/or nests are necessary to support this most unusual extension of breeding range.

Townsend (1968) reported positive evidence of breeding for eight species of land birds: Ring-necked Pheasant (*Phasianus colchicus*), Horned Lark, Rock Wren, House Sparrow (*Passer domesticus*), Western Meadowlark (*Sturnella neglecta*), Brewer's Blackbird (*Euphagus cyanocephalus*), and House Finch. Two of these were introduced by man, either directly or indirectly (pheasant, House Sparrow), and occupied man-modified habitat; two species (meadowlark and 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. The establishment of a permanent military station and the removal of the sheep which previously had overgrazed the sparse grass cover are probably the most important alterations since the early 1900s. The other four breeding species (Horned Lark, Raven, Rock Wren, and House Finch) are *the same presumed or proven permanent resident species recorded 66 years earlier by Grinnell.* Thus, here, as on most of the Channel Islands, there appears to be a stable core of species with very low probabilities of extinction. When inappropriate records are removed, according to criteria described earlier, the calculated minimum equilibrium turnover rate is zero. This finding is highly significant, for San Nicolas is the sole island in the Channel Islands group for which reasonably complete early and recent surveys are available.

Diamond reported 50% turnover in the avifauna of San Nicolas between 1917 and 1968. This discrepancy between our respective calculations very likely reflects the influence of the nonequilibrium component of avifaunal turnover on an island with a complex history of disturbance.

AVIFAUNAL TURNOVER ON THE CHANNEL ISLANDS: A REINTERPRETATION

A complete assessment of Diamond's turnover figures is impossible in the absence of complete data on the identities of all the species involved and the specific evidence for breeding activity or extinction he used. However, certain conclusions are unlikely to be modified importantly by these data.

First, it is certain that Howell's (1917) paper is inadequate as a baseline and that Diamond made a number of unjustified assignments of previous breeding status. Second, it is clear that human-related activities have played a major role in the turnover which has taken place in the present century. Diamond's claim (1969:60) that "species changes due to changing habitats or effects of man are greatly in the minority" is unfounded, at least in the case of extinctions: 54% of the supposed extinctions which can be identified to species and island are most likely related to human activities. These account for a minimum of 45% of the total number of extinctions listed in Diamond's summary of turnover rates. When instances of "pseudoturnover" are removed from consideration, the percentage of extinctions related to human activity is much higher.

Finally, based on the inferred breeding status of bird species in 1917 vs. 1968, it is clear that Diamond greatly overestimated the minimal equilibrium turnover rates for the avifaunas of the various Channel Islands. Whether or not his figures for colonization are as inflated as those for extinctions, the main conclusions of his study are called into question. If the rate of arrival of new species is indeed as high as Diamond claims, then the avifaunas are not in a state of equilibrium because the colonization rate greatly exceeds the extinction rate. If, on the other hand, the avifaunas are (approximately) at equilibrium, then the colonization rates estimated by Diamond must be reduced to the point where they balance the extinction rates; this would result in a much lower overall turnover rate than the 17–62% per island per 51 years reported by Diamond. In our view, the latter possibility is more likely. Certainly there has

been some turnover of the Channel Islands avifauna, but the majority of the changes have probably been caused, or at least influenced importantly, by human activities. The residuum of clear-cut cases of equilibrium turnover is evidently quite small. The possibility remains, of course, that a number of undetected colonizations and extinctions occurred between the times of the 1917 and 1967–68 surveys, as noted by Diamond (1969:62). The frequency of these undocumented events (which might be termed "*cryptoturnover*") is virtually impossible to estimate from the data presently available. All that one can expect from a comparison of two widely spaced censuses is a *minimum* estimate of turnover (Diamond 1969:62); it is our contention that this minimum is much lower than Diamond has claimed.

AVIFAUNAL TURNOVER ON TROPICAL ISLANDS

Rates of turnover of bird species have been reported for two islands located in the tropics (Diamond 1971; Terborgh and Faaborg 1973). Each of these studies raises questions similar to those discussed in detail for the California Channel Islands. Of course tropical avifaunas contain relatively few migrant species, and this fact should serve to alleviate some of the problems associated with the assessment of resident status, but the fact that most tropical birds do not migrate does not mean that residency can be automatically assumed on the basis of mere observation of the presence of a species on a tropical island.

Karkar. Diamond (1971) studied the avifauna of this moderately large (146 square miles) island located 10 miles off the coast of New Guinea. To compute turnover rates, he compared the results of his field work with a group of specimens obtained in January–March 1914 by professional collectors. No field notes accompany the specimens, hence records are lacking for species seen but not collected. Diamond notes these drawbacks of the "baseline" survey but proceeds with his computations and concludes that 11 lowland species found in May–June 1969, but missing from the 1914 collection, are natural immigrants. None of these immigrations can be considered valid unless one is willing to accept the extremely unlikely propositions that (1) the early collectors saw every species present on Karkar, and (2) that every species seen was collected. Most ornithologists familiar with the problems of observing and collecting birds in difficult tropical terrain probably would agree that some,

and quite possibly all, of the "new" species were not taken by the early collectors because they were difficult to obtain (three large birds of prey and a rail, for example), or simply because they were not encountered. Also, large birds of prey are commonly skipped by collectors, even when they can be obtained, because they are troublesome to prepare, to store, and to transport. Of five supposed "extinctions," that is, species represented in the 1914 collection but not found by Diamond and his native helpers in 1969, we would especially question the reported absence of the two species of rails which easily could have been overlooked by even the most careful observer. Even the conclusion that three species of pigeons were missing in 1969 is suspect for an island as large as Karkar. Moreover, in the absence of breeding data for the earlier records, it is not certain that all these birds were residents. Avifaunal data such as these are simply inadequate for determination of turnover rates, and we conclude that no strong evidence has been presented which would indicate a high rate of avifaunal turnover on Karkar.

Mona Island. Incidental to their interesting and important work on niche relations and species diversity of the birds of Mona, an island situated in the Caribbean between Puerto Rico and Hispaniola, Terborgh and Faaborg (1973) estimated the rate of species turnover for the interval of 1892 to the present. Only a small avifauna is involved, and it has been surveyed on several occasions between 1901 (Bowdish 1902) and 1972 (Terborgh and Faaborg 1973). Terborgh and Faaborg carefully attempted to sort out and exclude records of probable vagrants and migrants in determining their lists of species.

Although the vegetation of Mona generally remains in good condition, hunting and mining activity, as mentioned by Terborgh and Faaborg, probably played an important role in the disappearance of the Hispaniolan Parakeet (*Aratinga chloroptera*), one of the three species which are thought to have become extinct during this century. The former breeding presence of another of these species, the Key West Quail-Dove (*Geotrygon chrysia*), was inferred solely on the basis of a sight record by Bowdish (1902). Bond (1961:109) questioned the record of this species on Mona and mentioned the occurrence of this quail-dove as a vagrant in the West Indies. Neither of these two reported extinctions satisfy the criteria for equilibrium turnover. The third extinction, Ruddy Quail-Dove

(*Geotrygon montana*), may be a valid example.

Three species have colonized Mona since the early surveys. These colonizations may have been unaided by human activities but it is reasonable to suggest that the presence of small agricultural clearings were crucial in allowing the establishment of at least one of the colonizing species, the Smooth-billed Ani (*Crotophaga ani*). The possible role of habitat disturbance in permitting the initial establishment of the White-winged Dove (*Zenaida asiatica*) and the American Kestrel (*Falco sparverius*) cannot be ignored. We conclude that there has not been a convincing demonstration of rapid equilibrium turnover on Mona Island, although some extinctions and immigrations have occurred.

CONCLUSIONS AND SUMMARY

A survey of the literature pertaining to minimum avifaunal turnover rates on islands has convinced us that such rates have been overestimated, sometimes by as much as an order of magnitude. It is surprisingly difficult to find adequate documentation for more than a few of the dozens of instances of equilibrium turnover which have been cited by various authors. Where an extinction or immigration is reasonably well documented, human influences are most often strongly implicated. A large number of supposed extinctions and immigrations which have been cited in the recent literature are examples of "pseudoturnover," based on improper evaluation of faulty or incomplete faunal data.

Banding records from the Farallon Islands confirm that, at least for continental islands at temperate latitudes, large numbers of individuals of numerous species appear throughout the year, not just during peak migratory periods. Without specific evidence of breeding activity, it is unwarranted to assume residency for bird species on such islands regardless of the time of year at which observations are made.

Notwithstanding wishful thinking to the contrary, the early surveys which have been used as baselines for comparison with modern studies do not provide a reliable data base for computing equilibrium turnover rates. Accordingly, the "minimum" turnover values of Diamond (1969, 1971) and Terborgh and Faaborg (1973) appear to be severely inflated. Whether avifaunal turnover rates on islands really are as high or higher than reported remains to be demonstrated.

Given the inherent limitations of the available early surveys a more fruitful alternative

to the comparison of "old" and "new" surveys would be to conduct more or less continuous monitoring of breeding bird populations on small or structurally simple islands under equilibrium conditions. 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.

Unfortunately, there is no easy way to verify all of the predictions generated by the Mac-Arthur-Wilson equilibrium model. The most satisfying tests of the theory (Simberloff 1969; Simberloff and Wilson 1969, 1970; Wilson and Simberloff 1969) have also been the most elaborate and painstaking studies undertaken in this field to date. Attempted shortcuts, often involving comparisons of brief recent surveys with incomplete older surveys, have not advanced our understanding significantly. Everyone appears to agree that some avifaunal turnover occurs under natural conditions on islands (see Mayr 1963, 1967), but the magnitude of such turnover is still very much open to question.

Detailed faunal data, carefully taken and critically interpreted, are the heart of any valid turnover study. Many questions raised in the present paper would be unnecessary if all authors attempting to demonstrate equilibrium turnover would recognize the necessity of publishing sufficiently detailed supplementary information to allow the reader to make an independent assessment of the validity of various claims involving colonization and extinction. As a minimum, such data should include: (1) the identities of all species involved; (2) the specific evidence upon which breeding presence or absence was inferred; and (3) the exact dates during which the field work was conducted.

We regret the necessity for the generally negative tone of these comments. Indeed, a respected colleague has offered a friendly admonition to the effect that our standards for acceptable faunal data are so stringent that, if generally adopted, they would prevent a lot of good research from being done. We are compelled to reply that we are unaware of any examples of good research in the area of faunal analysis which do *not* involve attention to detail and a realization of the inherent limitations of observational data.

The MacArthur-Wilson equilibrium theory has been a revolutionary influence in the fields of zoogeography and ecology. Certainly the theory is important enough to warrant impartial testing wherever this is possible.

Regarding the rate of equilibrium turnover in insular avifauna, the proper procedure is to adopt as a null hypothesis the proposition that no such turnover exists. This places the burden of proof in its proper place—on the shoulders of those who would establish the validity of the model in a given situation. But in the search for understanding, we would do well to contemplate Throckmorton's (1968: 369) reminder that "No one is so desperate for answers that he must risk borrowing them from fantasy."

ACKNOWLEDGMENTS

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