

HOW MANY BIRD SPECIES IN HAWAI'I AND THE CENTRAL PACIFIC BEFORE FIRST CONTACT?

JOHN CURNUTT AND STUART PIMM

Abstract. Since European settlement, extinctions of Pacific island birds have been widespread and well documented. Subfossil evidence indicates that the Polynesians caused extinctions of an even greater magnitude. Estimating the prehuman Pacific avifauna is difficult because the existing fossil record is inevitably incomplete. We use the theoretical framework of island biogeography to make estimates of the numbers of endemic rails, parrots, pigeons and doves that existed in the Pacific before human contact. We formulate two sets of estimates for each taxon by assuming that: (1) endemism is defined as a distribution limited to a single island, and (2) endemism is a distribution limited to a single-island group. These two assumptions lead to different results (884 compared with 242 endemic species). We refine our predictions by applying topographical and disturbance parameters. Our best estimate is that 332 endemic species of the three taxa once existed in the Pacific, of which 210 are not accounted for in the paleontological and historical data. Applying this ratio of known to missing species for all landbirds, we estimate the original Pacific avifauna to be composed of less than 1,500 species, of which approximately 230 survive. Our estimate of the original Pacific avifauna falls between two earlier conflicting predictions (800 and much greater than 2,000). Our predictions of the number of species missing on each type of island are testable. Our results can be used to focus research efforts on islands that are more likely to have held species of interest. Furthermore, our results can be interpreted to predict the risk of future extinctions that may result from habitat loss or rising sea levels.

Key Words: biogeography; doves; extinctions; Pacific Islands; parrots; pigeons; rails; sea level; tsunamis.

The Hawaiian Islands form one of the largest and most diverse archipelagoes in the Pacific. As a group, they lead the world in numbers of historically extinct and currently endangered species of birds (King 1985). This dismal legacy, however, did not befall the Hawaiian Islands alone. Untold bird extinctions doubtlessly occurred across the Pacific over the four millennia since humans first set sail there. What was the magnitude of the loss of bird species in the Pacific?

“The Pacific” denies an easy definition. Defined in the context of human settlement over the last 4,000 years, we will consider 41 island groups (Fig. 1). They span the Hawaiian Islands in the northeast, west to the Marianas and Palau, southwest through Vanuatu, south to New Zealand and east to Easter Island. Pratt et al.’s (1987) field guide covers all but Vanuatu (for which see Bregulla 1992), New Zealand (see Falla et al. 1983), and Easter (which has no extant landbirds).

There are roughly 240 extant native species of landbirds in this region (Falla et al. 1983, Pratt et al. 1987, Bregulla 1992). The largest families are Pachycephalidae (whistlers; 40 spp.), Columbidae (pigeons and doves; 34 spp.), Muscicapidae (Old World flycatchers; 28 spp.), Rallidae (rails; 21 spp.), Psittacidae (parrots; 19 spp.), and Fringillidae (Hawaiian honeycreepers; 19 spp.).

To the above number of species we must add

those that we know once existed but are now known only through historical records and fossils. Among the islands of the Pacific, the many vertebrate extinctions that occurred since the sixteenth century subsequent to the arrival of European explorers are well documented. For example, Diamond (1984) reported that, since 1600, Micronesia and Polynesia suffered roughly 100 bird species extinctions. The forces responsible for the loss of these species were the same as those that operate today, primarily habitat loss and the introduction of exotic species (Steadman 1997a,b). A much greater extinction event preceded the arrival of Europeans and was concurrent with the first human contact (Steadman 1997a,b). Beginning about 4,000 years ago with Melanesia and Micronesia and ending about 1,500 years ago with Hawai'i, Easter Island, and New Zealand, humanity brought the last habitable places on Earth under its domain (Rouse 1986).

European explorers found well-developed, agricultural-based societies on all of the larger Pacific islands. It is not known how many of the smaller, less suitable islands were visited only temporarily by the wandering islanders (Oliver 1961). Habitat loss and exotic species (including dogs and pigs) doubtlessly caused the extinction of many species of endemic birds on the permanently settled islands. Even on smaller uninhabited islands endemic species, many of them flightless rails that had evolved in the absence

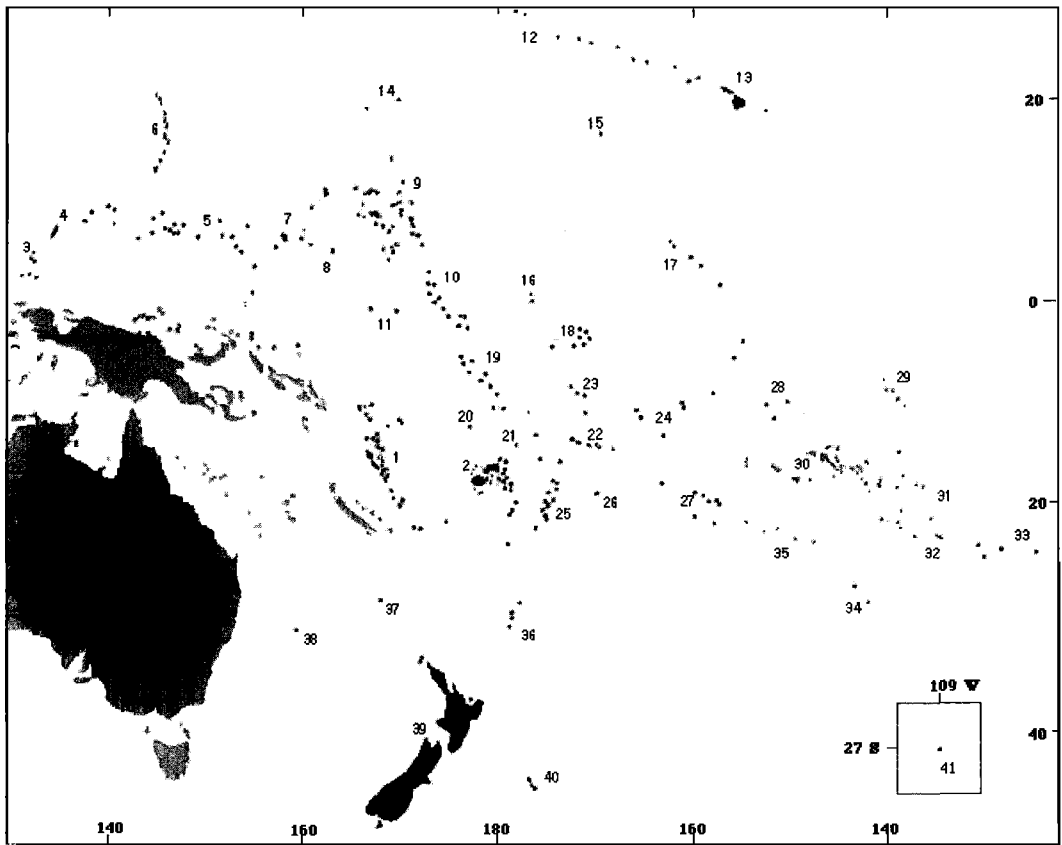


FIGURE 1. The islands of the Pacific. Numbers refer to island groups referred to in the text and listed in Table 1.

of terrestrial predators, could have been harvested to extinction by temporary human occupants.

We have evidence of these unrecorded extinction events in the fossil record (Olson and James 1982a, 1991; Milberg and Tyrberg 1993). Archeological efforts in Hawai'i by Olson and James (1982a, 1991; James and Olson 1991) and throughout the rest of the Pacific (Balouet and Olson 1987; Steadman 1991, 1992, 1993, 1997a,b; Kirch et al. 1995), have uncovered a large number of avian fossils that were deposited concurrently with early human occupation of the islands. Not all islands have been searched, and even if they were, it is unlikely that all extinct species would be found. Thus, the total number of extant and extinct species identified to date is an underestimate of the diversity of the prehuman Pacific avifauna.

An exact count of the number of landbird species known only as fossils is difficult to tally because they are not clearly enumerated in some published accounts. The Hawaiian Islands held 62 fossil species (James and Olson 1991, Olson

and James 1991) and New Zealand held 44 species (Steadman 1995). The other islands of the Pacific that have been searched held something less than 100 additional species (Steadman 1995). Thus, roughly 200 species of Pacific landbirds are known only from the fossil record.

Summing the number of extant, historically extinct, and prehistorically extinct (fossil) species, there are 540 known species of landbirds in the Pacific. This number is too low because the fossil record is incomplete. An accurate estimate of the prehuman Pacific avifauna depends on an accurate estimate of the "missing" fossil species.

Pimm et al. (1994) estimated the prehuman number of Pacific island landbirds by applying sampling analyses to fossil data. Briefly, given the number of species known only by fossils, those known by modern observations (i.e., those that still survive and those extinct since European colonization), and those known by both fossils and modern observations one can deduce the number of "missing" species from an island. Applying this method to data on the landbirds

of the tropical Pacific (including New Caledonia), Pimm et al. (1994) deduced that the number of known fossil species (ca. 200) is only half of the actual number of species that disappeared before European colonization. Pimm et al. (1994) estimated the original avifauna to include nearly 800 species of landbirds. Excluding data from New Caledonia and including data from New Zealand, to fit the boundaries to the current study, does not appreciably change these estimates.

A much higher estimate of the original Pacific avifauna was proposed by Steadman (1995, 1997). On finding fossil evidence of up to three or four now extinct species of flightless rails on islands he investigated, Steadman (1995, 1997a,b) suggested that the 800 major islands of the Pacific held more than 2,000 species of this taxon and lower numbers of other taxa—all driven to extinction as a result of first human contact. Steadman's (1995) approach set the question of original avifauna in the context of island biogeography.

In this paper we apply a robust theoretical framework, island biogeography theory (MacArthur and Wilson 1967a), to the Pacific islands to determine the number of islands that could have held endemic species of rails (Rallidae), pigeons and doves (Columbiformes), and parrots (Psittaciformes). We chose these taxa because they are well represented in the fossil record. Thus, we do not estimate the entire prehuman landbird fauna; instead our results can indicate the magnitude of the loss of bird diversity that has occurred since first human contact. We include in our analyses all named islands of New Zealand, Micronesia, central and eastern Melanesia, and Polynesia that experienced first human contact no earlier than 4,000 years before present (Rouse 1986). Unlike Steadman (1995, 1997), we incorporate data on habitat diversity, changing sea levels during the Holocene, and tsunamis. Each of these factors influences the effective size of islands for landbirds. Put simply, MacArthur and Wilson's (1967a) theory of island biogeography predicts more species on larger islands and those close to a source of immigrants, and fewer species on small or isolated islands. We perform two distance analyses: distance-from-source, as proposed by MacArthur and Wilson (1967a); and, distance between islands—isolated islands are more likely to produce species endemic to one island than those that have very near neighbors (Mayr 1963). By applying reasonable assumptions to this question, we hope to develop a more accurate estimate of the prehuman Pacific avifauna than has been produced to date.

We first identify those islands of the Pacific

that have the potential to maintain populations of landbirds. We then extrapolate the numbers of endemic rails, pigeons, and parrots that could have existed on all of these islands by applying the known maximum of each taxon recorded on different island sizes and types. In fact, we calculate two estimates of the number of endemic species by using two definitions of endemism. We then refine our estimates by considering ecological and environmental characteristics.

IDENTIFYING THE BIRD ISLANDS

We do not expect all islands of the Pacific to hold birds. Some islands are too small to support viable populations of landbirds. Some islands may also fall outside of the known range of the taxa we are investigating. These limitations to bird distribution are diagrammed in Figure 2. Our first task, then, is to estimate how many islands there are in the Pacific, and which of these could support a population of landbirds.

HOW MANY ISLANDS

No one knows how many islands there are in the Pacific Ocean. Estimates range from 30,000 to less than half of that number (Bryan 1963). The distribution of island sizes is fractal—that is, as one looks at the Pacific at finer scales, one finds more islands in a characteristic way. Thus, most islands are very small. We limited our data to named islands. We obtained gazetteer data (latitude, longitude, name) from the U.S. Defense Mapping Agency's (DMA) database available on the Internet. This search yielded 3,463 islands.

We assigned each island to an island group according to an arbitrary grouping scheme. Obvious archipelagos were identified as groups (e.g., the Gilbert Islands), as were single islands not obviously associated with an archipelago (e.g., Rapa). The result was 41 island groups (Table 1; Fig. 1). As described below, we first grouped islands that are very close to each other. Our primary reason for this was to add small islets to the larger islands that they surround and to unite many "islands" that occur as parts of individual atolls. Second, we determined which islands are too far from a source of immigrants for each taxon. Finally, we determined the size and topography of each island.

ISLANDS AND ISLETS

If two islands were near enough to each other to allow a species to move between them, then neither would produce an endemic species (Ricklefs and Schluter 1993). But how close is close enough? No data exist on this subject for birds in the Pacific. We know that the limiting distances between islands are surely taxon spe-

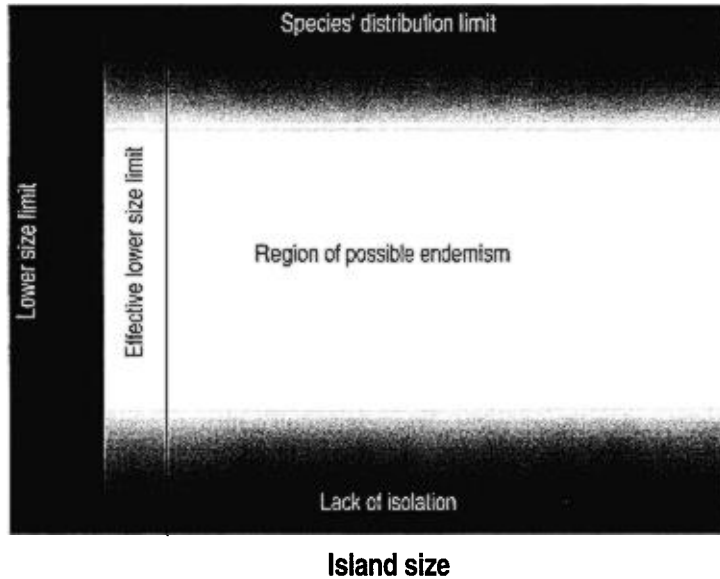


FIGURE 2. Theoretical framework for endemism of Pacific island birds. Islands that are too small to maintain persistent populations will not produce endemic species (lower size limit), nor will larger islands subject to inhibitory disturbance regimes (effective lower size limit). Some islands are close enough to allow genetic exchange between populations and will not produce endemic species (lack of isolation), while others lay outside of the distribution of some taxa (species' distribution limit).

cific and this, in turn, is affected by the mode and propensity of movement exhibited by each taxon. For the three taxa we consider in this paper, rails have a higher wing load (ratio of weight to wing area) than pigeons or parrots (Rayner 1988). Thus, it would take relatively more energy for a rail to fly a fixed distance than it would a pigeon. Left free to speculate, we chose a minimum distance equivalent to 0.1° of latitude or longitude (≈ 11 km at the equator) as sufficient for allowing isolation of breeding populations. We chose this distance primarily for ease of calculation, but also we feel that such a distance would provide an adequate barrier to movement for rails—the most stationary taxon because of its propensity to quickly evolve toward flightlessness (Trewick 1997).

We summed the sizes of all islands that were closer than 0.1° of latitude or longitude to each other. This grouping scheme reduced our data to 788 island sets. Hereafter, we refer to island sets as “islands.”

WHICH ISLANDS ARE TOO FAR

Landbirds are not distributed evenly across islands. Just as islands that are too close will prohibit divergence; islands that are too distant from a source population may not be colonized at a rate sufficient to allow persistence (Ricklefs and Schluter 1993).

We tested for the effect of distance-from-source on the distribution of each of our three taxa with multiple regressions. All of the taxa we consider in this paper have their origins in the Old World (rails: Ripley 1977; pigeons: Goodwin 1983; parrots: Forshaw 1977). We used Map[®] (Apple Computers, Inc.) software to determine distances between geographic centers of island groups and the following (geologically) continental source areas: Australia (Brisbane), Papua New Guinea (New Britain), Philippines (Manila), and Taiwan (Taipei). Since island size is the most effective predictor of species diversity (MacArthur and Wilson 1967a), we performed stepwise multiple linear regression of the number of species on total area of each island group, then added distance. We repeated this process for each of the distances generated from the four sources listed above.

At best, these multiple regressions only weakly explained the variation in species numbers with distance ($R < 0.2$) and were only significant for parrots and pigeons ($P < 0.05$). For this analysis, it is better for the data to speak for themselves. Figure 3 shows the distribution of rails, parrots and pigeons among the 41 island groups of the Pacific. Rails are found throughout the region, reaching the most remote groups including Hawai'i and Easter Island. Paradoxically, rails, for which even the largest ocean is not

TABLE 1. ISLAND GROUPS OF THE PACIFIC OCEAN INCLUDED IN OUR ANALYSES

Group	Group number	No. of island sets	Area (km ²)	Topography
<i>Melanesia</i>				
Vanuatu	1	38	11,400	H
Fiji Islands	2	74	1,860	H
<i>Micronesia</i>				
Palau	3	8	447	H
Yap	4	2	175	H
Chuuk	5	21	230	L
Mariana Islands	6	13	910	H
Pohnpei	7	2	360	H
Kosrae	8	1	100	H
Marshall Islands	9	28	255	L
Gilbert Islands	10	18	290	L
Nauru	11	2	36	L
<i>Polynesia</i>				
NW Hawai'i	12	2	8	L
Hawai'i	13	9	16,700	H
Wake	14	1	230	L
Johnson Atoll	15	1	2	L
Howland	16	1	10	L
North Line Islands	17	7	745	L
Phoenix	18	5	37	L
Tuvalu	19	6	27	L
Rotuma	20	1	49	H
Wallis and Futuna	21	2	275	H
Samoa	22	8	3,500	H
Tokelau Islands	23	3	13	L
North Cook Islands	24	5	10	L
Tonga Islands	25	18	563	H
Niue	26	1	258	L
South Cook Islands	27	9	234	H
South Line Islands	28	2	8	L
Marquesas Islands	29	11	1,062	H
Society Islands	30	10	1,710	H
Tuamotu Arch.	31	11	248	L
Gambier	32	6	21	L
Pitcairn Islands	33	2	8.5	H
Rapa	34	1	40	H
Tabuai Islands	35	4	120	H
Easter Island	41	1	170	H
Kermadec Islands	36	2	34	H
Norfolk	37	1	37	H
Lord Howe	38	1	10	L
New Zealand	39	33	267,800	H
Chatham Islands	40	4	1,085	H

"Group Number" refers to numbers shown on Figure 1. Island sets are named Islands that are within 0.1° latitude and longitude of each other. We include only those sets with combined areas of >150 HA. Topography is either high-relief (H) or low-relief (L).

large enough to prohibit colonization, can quickly evolve to flightlessness (Diamond 1991). The distribution of pigeons has apparently been limited by the vast expanses of ocean that isolate Hawai'i and Easter Island, for neither has apparently held this taxon. For Easter Island, the nearest island to have ever held a pigeon is Pitcairn (1,600 km), and for Hawai'i, it is the North Cook Islands (3,500 km). Parrots have been

found on Easter but not the Hawaiian Islands (nearest island with parrots—Marquesas, 3,800 km distant).

For our analyses, therefore, we consider all islands of suitable size as potential sites for rail colonization; all but the Hawaiian and Northwest Hawaiian Islands for parrots; and, all but the Hawaiian groups and Easter Island for pigeons.

SIZES OF ISLANDS

The final parameters we consider in determining which island sets could maintain populations of landbirds are size and topography. We obtained data on the sizes of islands from various sources in the literature and from direct measurements from maps (ranging in scale from 1:10,000 to 1:300,000). Some islands listed in the DMA database were not found on maps (or referred to in any literature we searched), thus, we have no data on their sizes. However, we are confident that we have size estimates for all of the major islands (i.e., > 2 km²) and for many lesser islands, and those with missing data are from the smallest size classes. Our confidence lies in the fact that island sizes fall within a class of negative exponential distributions known as Zipf-Mandelbrot (Fairthorne 1969). For the islands for which we have data, we plotted the size distributions on log-log axes. The Zipf-Mandelbrot distribution predicts a straight line for this graph (Fig. 4), and we can interpret deviations from the linear fit as "missing" islands. By extending the linear fit below 1 km² to our smallest recorded island size (10 ha), we predict that about 800 islands are missing from our island size data set.

While landbirds do occur on very small islands in the Pacific, these are members of satellite populations of larger nearby islands. For example, the Antipodes Island Parakeet (*Cyanoramphus unicolor*) is found in low numbers on Archway Island (6 ha)—the smallest of the Antipodes Islands (Taylor 1985). The species is also found on the 54-ha Bollons Island, which is much less than 1 km from Archway Island. The greatest part of this species' population, however, is on the 20 km² Antipodes Island—about 1 km from Bollons. The loss of the Antipodes Island population would probably lead to the eventual extinction of this species. It would not make ecological sense to identify Archway Island as one suitable for sustaining a population of parrots. Similarly, we can safely ignore the existence of the 800 "missing" islands in our data because they are too small to hold endemic species of landbirds.

The smallest Pacific island known to hold an endemic rail is Wake Island, 6.5 km² and home

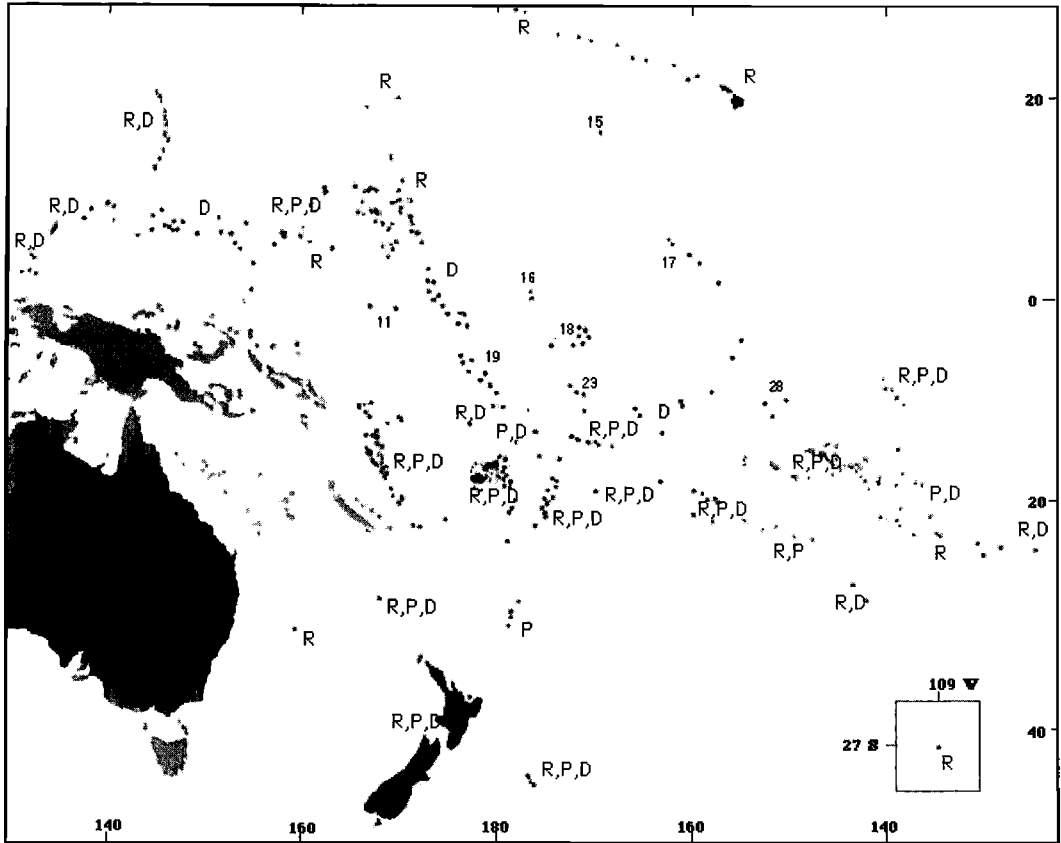


FIGURE 3. The distribution of rails (R), parrots (P), and pigeons and doves (D) among the Pacific islands. Numbers correspond to group names in Table 1 and indicate island groups that hold none of the three taxa mentioned above.

to *Rallus wakensis*. The smallest island to hold an endemic pigeon is 28 km² Maketea (Tuamotu Archipelago), home to *Ptilinopus chalcurus*; and the smallest island to hold an endemic parrot is Norfolk Island (33.7 km²) where remains of *Nestor productus* have been recovered.

These minima may not be actual; all islands have not been sampled. We performed a Monte Carlo simulation (Efron and Tibshirani 1993) to predict the minimum size of an island that should support an endemic species from the observed distribution of island sizes with endemic species. Using data on island sizes, we randomly selected a number of islands equivalent to the number that we knew held endemic species of each taxon. For example, 23 islands held at least one endemic species of rail. We randomly selected 23 islands from the entire set of 834 and recorded the minimum size of this subset. We then calculated the mean minimum value of 100 repetitions. By repeating this process with increasing cutoff values applied to the entire data

set, we determined the lower 95% confidence limit within which our known minimum island size fell (Fig. 5).

Some islands have held more than one endemic species of a taxon. For parrots and pigeons there were one and two islands, respectively. For these taxa we could not perform the above described simulation to determine the minimum island sizes for two or more species—the sample size is too small. For rails, however, of which 10 islands held more than one endemic species, we could estimate the minimum island size for two species by applying the simulation (with a sample size of 10). To determine which islands could have held more than two species of rail (or more than one species of parrot or pigeon), we assumed that the smallest island for which we had data was the actual minimum.

TYPES OF ISLANDS

Our measure of habitat diversity was very coarse. We described islands as “high-relief” or

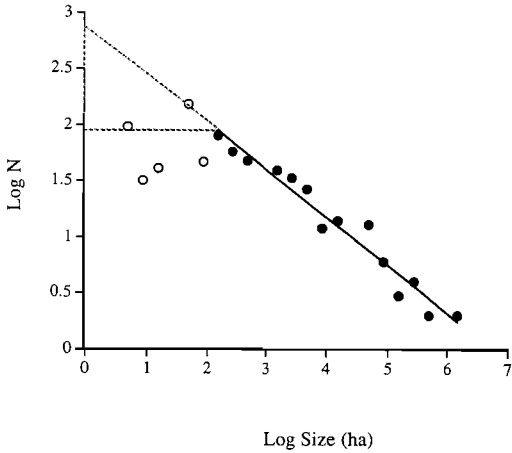


FIGURE 4. The relationship between island sizes and their frequency. The linear fit was calculated after excluding the two smallest size classes (open circles) and the three largest size classes (not shown). The area within the triangle represents islands with size data missing from our data set, assuming island sizes exhibit a Zipf-Mandelbrot distribution.

“low-relief.” High-relief islands were those described in the literature as volcanic, hilly, or mountainous or whose representation on maps included hachures. Low-relief islands were all of those described as atolls or were lacking hachures on maps that normally include such data. High-relief islands are rich in habitat diversity compared to low-relief islands (Adler 1992). We apply the same topography to entire groups by summing the areas of all islands within groups and defining them as high relief if > 50% of the total area is attributed to high-relief islands.

EXTRAPOLATING ENDEMICS

To estimate the potential number of endemic species that each taxon held, we determined the known maximum number of endemics (living and fossil) on islands of different sizes and topographies throughout the Pacific. After estimating the size of the smallest islands which we would expect to find endemics on, we used these numbers to predict the maximum numbers of endemic species with reference to the distribution of island sizes and topographies within each island group (Fig. 6). We tallied the number of known endemics and the number of predicted endemics across taxa for each island group then

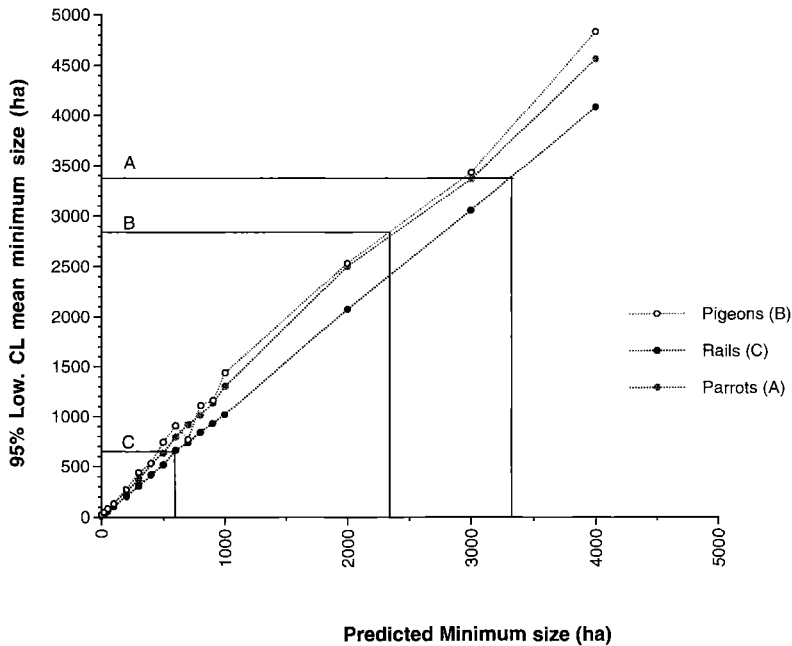


FIGURE 5. Results of a simulation whereby we randomly selected a number of islands equivalent to the number occupied by endemic species of each taxon. The x-axis represents the lowest value in the data set for each simulation, the y-axis is the 95% lower confidence limit of the mean of 100 repetitions. A, B, and C represent the actual minimum sizes for parrots, pigeons, and rails, respectively. The vertical lines intercept the x-axis at the smallest island size we would expect to find endemics of the respective species.

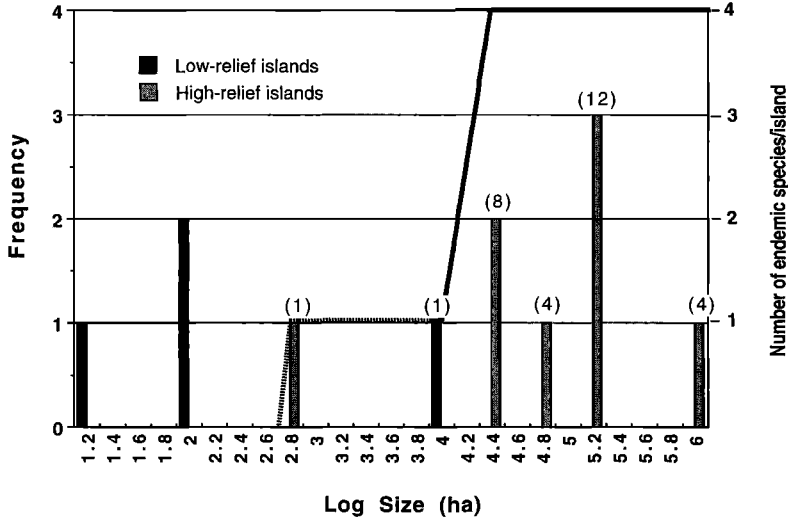


FIGURE 6. The size distribution of islands of the Hawai'i group classified as high relief and low relief. The solid line indicates the maximum number of endemic rails found on all high-relief islands in the Pacific while the dashed line indicates maxima for low-relief islands. We multiplied the maxima for each size class by the number of islands in each size class to predict the number of endemic rails that could have existed in each island group. Numbers in parentheses indicate the number of rails expected for each island size X the number of islands.

calculated the proportion of missing endemic species.

Our use of maxima reflects the potential lack of fossil data on some islands. For example, well-searched Mangaia of the South Cook Islands group held four endemic rails. Tofua of the Tonga Islands, with a similar size and topography, revealed none. For our estimates we assume that Tofua held four endemic rails. This may be incorrect; to paraphrase Montaigne, speciation is not so often the result of great design as of chance. There may never have been endemic rails on Tofua simply because no rails have survived there long enough to speciate.

Since the true number of prehistoric endemics cannot be known, we must be content with estimating this number by setting realistic limits based on the available data. Of the four factors we consider as affecting endemism, we have data on absolute lower island size and distance from source. Data do not exist for two other factors—effective lower island size (disturbance effects) and the minimum distance between islands needed to produce endemism (dispersal effects). Thus, we are left with the familiar quandary of decreasing our certainty as we increase the number of parameters. We address the problem of prehistoric disturbance on a group by group basis later. Our approach to effective distance between islands is as follows.

As noted earlier, we grouped all islands 11 km or closer to each other into sets. While an 11

km expanse of ocean may prohibit the movement of a flightless rail, it may have less effect on a strong-flying pigeon. We could further group our islands by different distances for each taxon, but this would be a series of educated guesses at best. Instead, we approach this problem by determining the maximum number of endemics that we know to occur in each island group. For example, the Red-bellied Fruit Dove (*Ptilinopus greyii*) is found on 28 islands of the Vanuatu group (total area of 11,000 km²). Thus, it does not fit our definition of a single-island endemic. It is, however, found only in the Vanuatu group, so it does exhibit a form of endemism. In Vanuatu, this species is found on both low- and high-relief islands. We conclude then that any island group that is dominated by high-relief islands and has a combined area the size of the Vanuatu group would hold an endemic pigeon.

We, therefore, produce two estimates for each taxon—the number of endemics at single islands and the number of endemics at island groups. The true number of endemic rails, pigeons, and parrots that have existed in the Pacific probably falls somewhere between these two values.

THE BIRDS

We chose rails, parrots, and pigeons for our analyses because they are well represented in the fossil record. We reviewed all available literature on the distribution of extant, historically ex-

TABLE 2. AN ESTIMATE OF THE NUMBER OF RAIL SPECIES IN THE PACIFIC BEFORE HUMAN COLONIZATION

Island size and topography	Number of islands	Number of species/island	Predicted total number of species
<600 ha, high and low relief	578	0	0
600–1000 ha, high and low relief	44	1	44
<1000 ha, low relief	61	1	61
1000–6400 ha, high relief	86	2	172
<6400 ha, high relief	65	4	260
Total	834		537

Maximum numbers of species are gleaned from the data for each size/topography of island. The predicted number of species is the product of maxima and the number of islands.

tinct, and subfossil species of these taxa in the Pacific. We assigned each species to all islands on which it was known to occur.

RAILS

Single-island endemics

We catalogued 55 species of rails known to have occurred in the Pacific. Of these, only five (all extant) are not restricted to either single-island sets or single-island groups. Two-thirds of the species are known only from fossil data and 65% are endemic to one island. Endemic rails are found on only 13 of the 41 island groups

The results of our simulation show that the smallest island with an endemic rail (6.5 km²) falls within a distribution that has a lower 95% confidence limit of 6 km². Both high- and low-relief islands have held single endemic species of rails, thus, we expect that all 256 islands that are larger than 6 km² held at least one species. Ten islands, all high relief, held more than one endemic species. The smallest of these was Lord Howe Island (10 km²), which held two species, followed by Mangaia (64 km²), which held four. Since four species of endemic rails is the maximum we encountered, we apply this value to all larger islands. Table 2 and Figure 6 illustrate our method of prediction of the number of rail species for the entire Pacific and specifically for the Hawaiian Island group.

We performed the same analysis on each island group and estimated that approximately 537 endemic rail species existed in the Pacific, of which 482 are not accounted for by a living or fossil species. Over one-third (36%) of the missing endemics are attributed to only two groups—Vanuatu (94) and Fiji (86). Whereas 13 groups hold no endemics nor are expected to, 14 others hold none but should. Of the remaining 13 groups, 11 hold fewer endemics than expected, and two (Wake Island and Lord Howe

Island) hold the number of endemics we predict (one and two, respectively).

Island-group endemics

Eleven of the 55 species of rails in the Pacific are endemic to groups of islands. The occurrence of the Wake Island Rail (*Rallus wakensis*) on Wake Island, an island group in itself, insures the expectation of at least one endemic rail on all low-relief groups except Johnston Atoll, which is too small. For groups with high-relief islands, the maximum number of endemics ranges from two for groups as small as 10 km² (Lord Howe) to 12 for groups larger than 16,700 km² (Hawai'i). Summing over all groups, we expect 143 endemic rails in the Pacific based on our island group analysis.

PARROTS

Single-island endemics

Of the 24 species of parrots we catalogued, 9 are endemic to single islands. The majority of these (5) are found in the southwest Pacific. No low-relief islands hold endemic parrots. Norfolk Island (33.7 km²) represents the smallest island to hold an endemic parrot (*Nestor productus*). We estimated that the lower size limit of islands that would support endemic parrots is 28.5 km². Excluding the Hawaiian islands and Easter Island, there are 110 high-relief islands of 28.5 km² or greater. The only island with more than one species of endemic parrot is the largest in our data set—South Island, New Zealand (149,000 km²). Thus, we attribute three species to this island only, for a total of 94 species ([91 islands * 1 species] + [1 island * 3 species]).

Island-group endemics

In contrast to the rails, a large proportion of parrot species (30%) in the Pacific show endemism to single groups of islands. The smallest group to hold an endemic is Norfolk (34 km²), home to *Nestor productus*. We apply this value of one endemic to 18 of the 22 island groups that contain high-relief islands. We predicted two endemic parrot species to Vanuatu and Fiji. New Zealand held four endemics. The total number of endemic parrots we expect from our analyses of island groups is a mere 29 species.

PIGEONS AND DOVES

Single-island endemics

We catalogued 43 species of pigeons and doves in the Pacific. Only nine of these are endemic to single islands. Of these, five are known only from fossil remains and are identified only to genus. Huahine of the Society Islands held the highest number of endemics with three of

the unknown species (*Ducula* sp., *Gallicolumba* sp., and *Ptilinopus* sp.). Henderson Island of the Pitcairn group held two endemics—the extant Henderson Island Fruit Dove (*Ptilinopus insularis*) and a fossil *Gallicolumba* sp. The remaining four endemics were found on Rapa (Rapa Fruit Dove, *Ptilinopus huttoni*), Mangaia of the South Cook Islands (*Gallicolumba* sp.), Makatea of the Tuamotu Archipelago (Makatea Fruit Dove, *Ptilinopus chalcurus*), and Espiritu Santo of the Vanuatu group (Santa Cruz Ground Dove, *Gallicolumba sanctaerucis*).

The smallest island to hold an endemic was Makatea of the Tuamotu Archipelago. Makatea is 28 km² and low relief. We estimate that the smallest island likely to hold an endemic pigeon or dove would be 20.7 km². Islands with more than one endemic are Henderson (36 km²) with two species and Huahine (75.5 km²) with three—both of these islands are high relief. Again, excluding Easter Island and the Hawaiian groups, our estimate of the total number of endemics is thus: (53 islands * 1 species) + (25 islands * 2 species) + (50 islands * 3 species) = 253 species.

Island-group endemics

Just as we saw that a greater proportion of parrots showed endemism to groups of islands than the less mobile rails, a full 51% of the pigeons and doves are restricted to single-island groups compared to 30% for parrots. Thus, there appears to be a positive relationship between flight ability and area over which endemism extends.

Vanuatu held the most species (6) of pigeons and doves that were restricted to an island group, and the Marianas held the next highest number (5). These, and the other large groups of islands (Chuuk, Fiji, New Zealand, the Society Islands, and Tonga) account for 39 of the total 64 species of island-group endemic pigeons and doves. Unlike parrots, endemic pigeons and doves are also found on large low-relief groups. Two species are restricted to the Tuamotu Archipelago, a fact that leads us to predict the same number of species on the Marshall Islands.

THE ESTIMATED NUMBER OF ENDEMIC SPECIES

Our exercise produced two sets of estimates of the number of endemic species in each of three taxa. For estimates based on single-island endemism, we predict 537 species of rails, 94 species of parrots, and 253 species of pigeons and doves for a total of 884. We can account for only 57 single-island endemic species of the three taxa as either fossil, extinct or extant. Estimates based on island-group endemism yield 145 species of rails, 29 species of parrots, and 64 species of pigeons and doves (Fig. 7). We

can account for 40 of these as fossil, extinct, or extant. Thus, we predict that the total number of endemic species of these taxa that once occurred in the Pacific falls between 242 and 884.

TESTING THE MODELS: KNOWN VERSUS ESTIMATED ENDEMICISM

We may now investigate factors that would refine our predictions. Which estimates better reflect the known distribution of endemic rails, parrots, and pigeons and doves in the Pacific—those derived from single-island endemics or those from island-group endemics? To answer this question, we compare our predicted values with the known distribution of endemic birds.

We calculated two indices of the proportion of total missing endemics (all taxa combined) per island group, one for each of our definitions of endemism. We added 1 to all values of the total number of endemics known to exist and to the totals predicted from our two definitions of endemism. We did this so that we could calculate proportions (number of known endemics/number of predicted endemics) without having zero values in either the numerator or denominator. We arcsine transformed the proportions to make the distribution normal and ranked the results. We then compared the ranks by performing a linear regression of single-island endemic ranks on island-group endemic ranks (Fig. 8).

Not surprisingly, the linear fit was significant ($F = 18.37$, $P < 0.01$). The slope was less than unity ($b = 0.56$) suggesting that when the predicted number of endemics corresponds with the actual number of island-group endemics, the single-island prediction is low and vice versa. We tested for the influence of the number of islands in each group on both of our predictions. Neither set of predictions correlates with this parameter ($r < 0.2$ for both). Identifying each group as high relief (50% of total area is high relief) or low relief reveals the pattern responsible for the disparity between the two sets of ranks (Fig. 9). Predictions correspond best with known endemism for low-relief groups when endemism is defined as a single-island distribution. Conversely, for high-relief groups, predictions based on group endemism correspond best with the number of known endemics. We believe there are ecological reasons for this.

Groups of low-relief islands tend to have smaller islands than high-relief groups (ANOVA: $F = 4.21$, $P = 0.04$). For low-relief groups, an individual island approach to endemism would successfully identify those few large islands in the group that could support a large population of birds. In contrast, predictions based on group endemism would lead to overestimates because the area across each group is

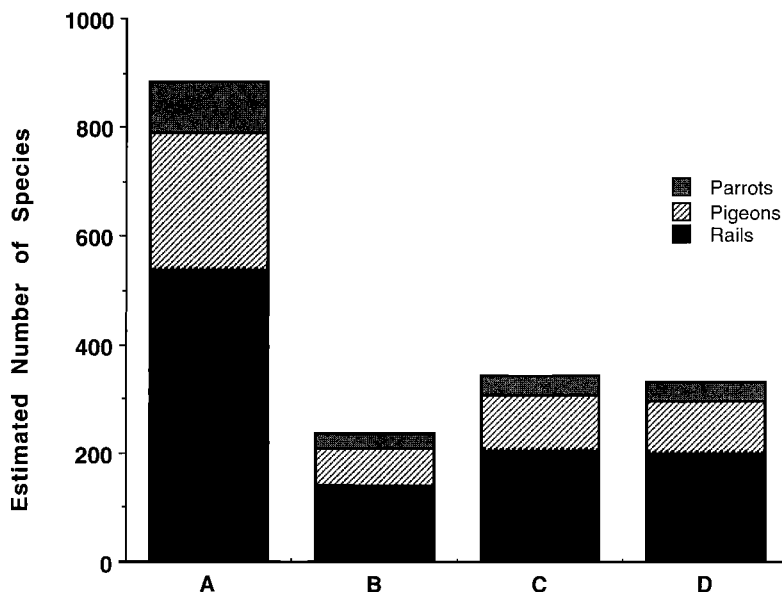


FIGURE 7. Total predicted numbers of endemic rails, parrots, and pigeons in the prehistoric Pacific under four sets of assumptions: (A) endemic species are those that occur on only one island; (B) endemic species are those that occur within single-island groups; (C) low-relief island groups produce endemic species at single islands and high-relief island groups produce endemics at island groups; and, (D) the same as (C) with modifications driven by patterns of disturbance (sea-level change and tsunamis).

summed. Conversely, the assumption of single-island endemism for the larger islands of high-relief groups ignores factors that potentially limit the size of bird communities. In his analysis of the assembly of the fruit-pigeon guild in New

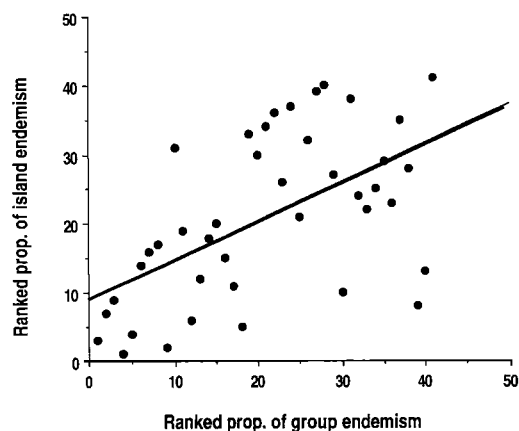


FIGURE 8. Ranked proportions of predicted numbers of endemic birds (rails, parrots, and pigeons combined) over known numbers of endemics. Values on the y-axis were generated using the assumption of single-island endemism while those on the x-axis were generated with the assumption of island-group endemism.

Guinea, Diamond (1975) showed that the entire species pool is never found in one locality. Some species never occurred together and some sets of species excluded particular species. This effect is primarily due to competition between species with closely related niches. Another ecological factor that over inflates the estimates for high-relief islands stems from our grouping across taxa. Some high-relief islands may provide habitat for each of the three taxa we discuss, but it may be unreasonable to assume that all of them do.

We can now refine our original estimates of endemism by calculating the totals for each taxon separately for low- and high-relief island groups using the appropriate assumptions of endemism (low-relief and single-island endemism; high-relief and island-group endemism). This yields 206 species of rails, 38 species of parrots, and 101 species of pigeons and doves (Fig. 7). These sum to 345 species across taxa.

WHERE THE ENDEMICS ARE AND WHERE THEY ARE NOT

Five island groups (Johnson Atoll, Howland, South Line, Gambier, and North Cook) are all low relief. They have no endemic species, nor are expected to under the assumption of single-island endemism. Our interpretation of the re-

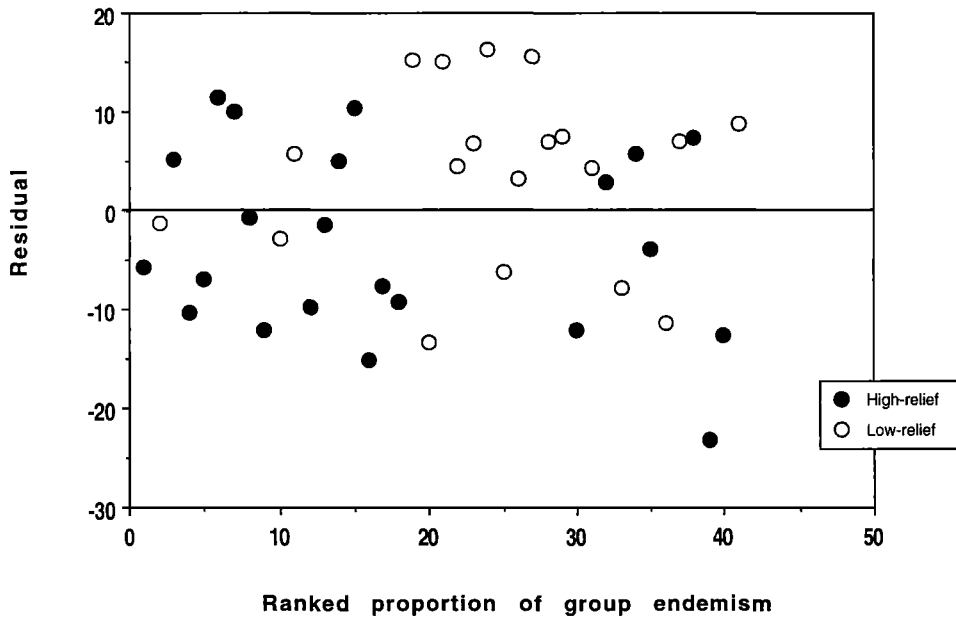


FIGURE 9. Residuals of the linear relationship of predicted endemic species under single-island endemism versus island-group endemism (Fig. 8) with each island group defined as either high or low relief.

results for the remaining 36 island groups depends on two assumptions. First, the maximum number of endemics recorded represents the actual maximum of each taxon that could occur on each type of island and, second, the recorded maxima on each island size/topography are applicable to all islands in each class. There is a chance that the first assumption is incorrect. Continued excavation of subfossil remains may well produce more species of birds, even on islands that are already well represented with endemics. The second assumption ignores differences in the history of islands across the Pacific. While there is little we can do to refine our predictions in light of the uncertainty of the first assumption, we can investigate the history of the Pacific islands to uncover patterns of species numbers on island groups.

The name "Pacific" belies this ocean's violent history. Natural disturbance of the Pacific islands can be a potentially limiting factor in speciation among birds. Stoddard and Walsh (1992) list five environmental factors that influence island ecosystems: volcanicity and earthquakes, sea-level change, tsunamis, rainfall patterns, and hurricanes. We investigate two of these: sea-level change and tsunamis. We chose these factors because they operate at regional scales, their effects are unambiguous, and they occur across a temporal scale that is consistent with evolutionary time.

SEA-LEVEL CHANGE

A number of studies concerning sea-level change in the Pacific over the last 10,000 years have been reported in the literature (Ota et al. 1988, Pirazzoli and Montaggioni 1988, Yonekura et al. 1988, Pirazzoli 1991). Throughout the Pacific, sea level was much lower 10,000 years before present (BP) than any time since. At that time, global sea levels were rising rapidly with the melting of the glacial ice sheets. Indeed, the massive infusion of water into the oceans led to regions of hydroisostasy (depression of the ocean floor by water loading) and consequent elevated sea levels (Pirazzoli 1991). Thus, from 6,000 BP to as late as 1,200 BP some island groups had sea levels significantly higher than at present.

During the last glacial maximum (18,000 BP), when sea levels were nearly 150 m lower than today, all islands of the Pacific were larger. For example, the Fiji group currently has a combined area of 18,600 km², whereas at 18,000 BP its area was over 35,000 km² (Gibbons and Clunie 1986). With rising sea level there would have been a loss of area and habitat. Thus, many island groups probably held more endemic species in the distant past than they did even in prehistoric times. Isostatic effects have been recorded for French Polynesia, the South and North Cook Islands, and the Marquesas Islands

(Pirazzoli and Montaggioni 1988, Yonekura et al. 1988, Stoddard and Walsh 1992; Table 2). As late as 1,200 BP, these groups exhibited less surface area than today—with groups such as the Tuamotu Archipelago disappearing almost completely (Gibbons and Clunie 1986).

This scenario raises two important considerations for our estimates of the prehuman avifauna. First, the decrease in area of many large islands that began at 18,000 BP would have caused a decrease in the number of bird species. This decrease may not have been contemporary with the decrease in area. Diamond (1972) showed that the reduction of one large island, the D'Entrecasteaux Shelf, into a number of small fragments should have led to a reduction of the number of bird species to a new equilibrium. However, he suggests that the time to reach the new equilibrium is dependent on the size of the new island. Thus, there could be a lag time (of several thousands of years in the above case) before the actual species numbers reflect the restraints of the size of the new island. We are not aware of any studies similar to Diamond's (1972) that address the islands included in our analyses. We will assume that the avifauna of the islands was at equilibrium at 4,000 BP. In doing so, we risk underestimating the number of species on all islands but those affected by the above mentioned isostatic effect; for these islands, our estimates would be to high.

The second consideration regarding sea level and endemism is the effect of elevated sea levels on low-relief islands. The low-relief island groups of Gambier, North Cook, and the Tuamotu Archipelago were affected by isostatic sea levels (Table 3). Of these, only Tuamotu is expected to have single-island endemics. We predict six species of rails and six species of pigeons—one pigeon exists (*Ptilinopus chalcurus*). Of this group's 60 islands, only five are greater than 30 km². Apparently, this species was able to survive the elevated sea level of 6,000–1,200 BP among these islands. The Fiji group is dominated by large high-relief islands but also holds a large number of surrounding low-relief islands. This group experienced sea levels nearly 2 m higher than present as late as 2,500 BP (Gibbons and Clunie 1986). Endemism would have been improbable in these islands up to that time because of the lower extent of the area. We predict that eight species of pigeons and 16 species of rails could have inhabited these low islands—none are known to have existed there. We removed the low-relief islands from the total area and calculated the number of endemic species we would expect on Fiji based on group endemism. This had no effect on our predictions. The size of Fiji's high-relief islands

TABLE 3. ISLAND GROUPS FOR WHICH PUBLISHED DATA EXIST ON MEAN SEA LEVELS (RELATIVE TO PRESENT; IN METERS) AT THREE PERIODS OF THE HOLOCENE (FROM PIRAZZOLI 1991); MAXIMUM SEA LEVEL AND TIME OF OCCURRENCE (OTA ET AL. 1988, PIRAZZOLI AND MONTAGGIONI 1988, YONEKURA ET AL. 1988, PIRAZZOLI 1991); AND MAXIMUM TSUNAMI RUN-UP HEIGHT (NATIONAL GEOLOGIC DATA CENTER)

Group	Mean relative sea level			Maximum sea level	Maximum run-up
	Years before present × 10 ³				
	10	5	2.5		
<i>Melanesia</i>					
Vanuatu					0
Fiji		+1	0	2 (2500)	5.9
<i>Micronesia</i>					
Palau					0
Yap					1.9
Chuuk	-40	-2	-1		
Marianas		+4.5	+2.4		1.9
Pohnpei	-40	-5	-2		
Marshalls			+2.4		0
Gilbert		-3	+2.4		
<i>Polynesia</i>					
Hawai'i	>-15	0	0		16.8
North Line					0
Tuvalu			+0.6		
Samoa		-5	-2		1.9
North Cook				1 (1500)	0
Tonga					0
South Cook	-17	-1	+1	1.7 (3400)	0
Marquesas				1 (1500)	9
Society	>-20	+0.5	+1	1 (1500)	3.4
Tuamotu	>-20	+0.9	+0.9	1 (1200)	2.3
Gambier				1 (1500)	
Pitcairn					0
Rapa				1 (1500)	1.8
Tabuai				1 (1500)	
Kermadec				0	12
Norfolk				0	
New Zealand				0	5.9
Chatham				0	0

are near the maximum for the Pacific, and the removal of the low-relief islands did not lead to a change of the maximum number of species expected.

Johnson et al. (1996), investigating the evolution of cichlid fish, reported the most rapid vertebrate speciation known—on the order of 3,000 years. Thus, high sea levels up to 1,200 BP must have reduced bird speciation on some Pacific islands. The effect of our sea-level analyses on our predictions results in the removal of five species of pigeons and six species of rails from our total.

TSUNAMIS

Tsunamis are a series of high-energy waves propagated by a major displacement of earth un-



FIGURE 10. Areas affected by tsunamis (shaded) and the direction of tsunamis (arrows) in the Pacific from 1900 to 1983 as reported in the Worldwide Tsunami Database (Lockridge and Smith 1984).

der the sea. They can have devastating effects on islands. For example, in the early morning hours of 1 April 1946 an earthquake in the Aleutian Islands, Alaska, caused a tsunami. Within minutes a manned lighthouse on Unimak Island had been obliterated with all hands lost. Four and a half hours later and over 3,000 km away the same tsunami hit the Hawaiian Islands. Reaching a maximum run-up height of nearly 17 m, it smashed into the Island of Hawai'i taking another 241 lives. This same series of waves caused casualties and property damage in California and as far south as central Chile (Lockridge and Smith 1984, Myles 1985).

Tsunamis of this magnitude are frequent with 14 occurrences in the Pacific Basin from 1900 to 1983 (Lockridge and Smith 1984). As with sea-level change, the effect of tsunamis on islands is variable. Islands without surrounding submarine shelves are more susceptible to remotely generated tsunamis because there is little to absorb the energy of the waves before they make contact. Topography and elevation above

sea level are also obvious factors in determining the effect of tsunamis on islands.

We accessed the Worldwide Tsunami Database, compiled by the National Geologic Data Center (<http://julius.ngdc.noaa.gov/seg/hazard/tsudb.html>), for recorded occurrences of tsunamis within our study site. Uninhabited islands are not well represented in the data set. For each occurrence we noted the location of the tsunami, its maximum run-up height, and its point of origin. We then classified our island groups as either susceptible to tsunamis or unaffected (Table 3).

The earliest recorded tsunami in our study area occurred in 1843. Since then over 130 tsunamis have been recorded. The Hawaiian Islands have seen the most tsunamis, a result of their central location relative to areas of seismic activity around the Pacific Rim and the lack of any energy-absorbing shelves around the group. Figure 10 shows regions affected by tsunamis and, when known, the direction traveled by tsunamis from their point sources.

We have data on tsunamis for 21 of our 41 island groups. Ten of these, however, have maximum recorded run-up heights of zero. That is, tsunami events do not noticeably affect these groups. Many of these fortunate island groups are low relief, including the extensive Marshall Islands. Ten of the remaining eleven groups are high relief and have experienced run-up heights from less than 2.0 to 16.8 m. The sole low-relief group affected by tsunamis is the Tuamotu Archipelago with a maximum run-up of 2.3 m.

The disturbance caused by tsunamis on high-relief islands is primarily limited to coastal areas, below the altitudinal distribution of most of the species we are concerned with. The effect of tsunamis on the fauna of the Tuamotu Archipelago, however, could be devastating. Most of the islands of this group are only a few meters in elevation, and the combined effect of higher sea level during the mid- and late-Holocene with tsunamis helps explain why this group has fewer endemics than we predict based on its size and topography. Finally, the Tonga group experienced a maximum run-up height of 4.0 to 6.0 m. This group is dominated by high-relief islands; however, 193 km² of its total 563 km² consists of low-relief islands. Assuming tsunamis were frequent and devastating enough to prevent endemism on these low islands, we can calculate a refined estimate of the number of endemics for this group by excluding all low-relief islands. This exercise results in the loss of one species of rail and one species of pigeon, leaving 35 rails, 12 pigeons, and 4 parrots attributed to the Tonga group.

Combining the effects of sea-level change and tsunamis, we can refine our previous estimate of predicted endemic species in the Pacific as follows: 199 endemic rails, 38 endemic parrots, and 95 endemic pigeons and doves (Fig. 7).

PROBLEM GROUPS

Even after incorporating the above adjustments to our predicted numbers of species, actual species account for less than half of the predicted numbers for 13 of the 23 high-relief groups. Six groups (Rotuma, Tabuai, Wallis and Futuna, Yap, Tonga, and Kermadec) have no actual island-group endemics although we predict from two to five species for these groups. For low-relief groups, 10 (Nauru, Northwest Hawai'i, Tokelau, Tuvalu, Gilbert, Niue, Phoenix, Chuuk, Marshall Islands, North Line Islands) have no actual single-island endemics although we predict from 1 to 20 species for these groups. In all, we predicted 210 species of rails, pigeons, and parrots that are not accounted for as either fossil, extinct, or extant.

DISCUSSION

We estimate that there were approximately 330 species of rails, pigeons, and parrots on the islands of the Pacific before human colonization began 4,000 years ago. Approximately one-third of these species are accounted for as either extant, historically extinct, or as fossils. Pimm et al. (1994), who looked for all landbirds, predicted that the fossil record was only half complete and that the original avifauna was about 800 species. In reviewing the fossil, historical, and current data, we could account for only one-third of the estimated number of species in the taxa we looked at. We should therefore apply a three-fold correction to the total number of known landbirds (540) and conclude that the entire Pacific landbird fauna was comprised of 1,620 or so species before human colonization. This simple multiplication, however, ignores differences in extinction rates between taxa. Steadman (1997a,b) suggested that flightless rails suffered a greater proportion of extinctions than any other taxon of birds. If so, an estimate of 1,500 species would be too high.

In comparing our results to Steadman's (1995) estimates, we must limit our consideration to rails—the only taxon that Steadman makes a quantitative estimate of. We estimate that the prehuman Pacific held about 200 species of rails, of which 21 are extant. Steadman's (1995) estimate (2,000+ species of rails) is an order of magnitude greater than ours. Like Steadman, we based our analyses on the roughly 800 larger islands of the Pacific. However, where Steadman simply multiplied a maximum number of rails per island by the number of islands, we incorporated into our analyses statistical probabilities and geographical, topographical and environmental data. Thus, we believe that Steadman's (1995) estimate of the prehuman avifauna is too high.

More fieldwork will inevitably bring new data to light. The discovery of more fossil species will potentially alter our estimates because of the multiplicative nature of our analyses. The discovery of one new fossil rail on a small island could conceivably add 800 to our current estimate of 200. This would still be half as much as the highest proposed number of rails (Steadman 1995). Currently, we suggest that the prehuman avifauna consisted of more than 800 and less than 1,500 species of landbirds. Further research (as outlined below) is needed to refine our estimates and to conserve the remaining species of the Pacific islands.

CONSERVATION CONCERNS

The loss to extinction of even our lowest predicted number of endemic species is disturbing.

Much more disturbing is the potential effect of this prehistoric loss on the biodiversity of the future. Habitat loss and the introduction of exotic species have had profound negative effects on endemic Pacific landbirds (Atkinson 1985, Pimm 1987). For rails, some of the progenitors of the clan of now extinct endemics may have themselves become extinct and anthropogenic disturbance on many islands may make recolonization by extant rails impossible. Thus, even for a rapidly speciating taxon like flightless rails, the potential for diversity has been greatly diminished.

Another conservation concern for Pacific landbirds is the rise of global sea levels. Although predictions of the rate of sea-level rise are rife with uncertainty, it is clear that global warming and subsequent rises in sea level will occur for centuries into the future (Hutter et al. 1990). Even with a moderate estimate of 4 to 6 cm per decade (Hutter et al. 1990, Wigley and Raper 1993) many low-relief islands will be inundated within the next few centuries.

FUTURE RESEARCH OPPORTUNITIES

Our predictions of the prehistoric Pacific island avifauna are testable. Using our results, researchers can focus excavation efforts on those islands that we predict will hold fossils of the greatest number of extinct species. Thus, we provide our analyses and results as a guide for continued work in this area of biodiversity. We conclude with the following suggestions for further study:

Where to look for subfossil birds

We predict that the greatest number of extinct landbirds existed on high-relief islands of at least 1 km² in size. The greatest part of the "missing" rails are from Fiji and Vanuatu. These areas should be surveyed intensely for

subfossil remains. Searches should, perhaps, also include island shelves that are currently submerged. Gibbons and Clunie (1986) make a strong argument for extending archeological excavations to these areas because they were exposed and possibly colonized during the human expansion into the Pacific.

Analyze the loss of potential species richness

A thorough understanding of the phylogenetic relationship between the landbird species of the Pacific would serve to identify the mechanisms of speciation and the ancestral species that most contribute to the potential diversity of each taxon. A molecular genetic analysis and mapping of the relationship of these species may also uncover phylogenetic differences in speciation rates, dispersal, and habitat utilization.

Predict the effects of rising sea level on current bird diversity

We have described the effect of area and topography on bird species diversity. Currently, models are available that predict changes in sea level both globally and regionally (Wigley and Raper 1993). The application of sea-level change projections to Pacific islands would result in predicted size distributions of islands, to which our approach can be applied. This will allow us to predict the expected loss of bird species in the Pacific in the coming century. These analyses, coupled with more traditional efforts (e.g., Franklin and Steadman 1991) could also be used to map a survival strategy for Pacific biodiversity in light of the threat of future sea-level rise.

ACKNOWLEDGMENTS

We thank M. Moulton, D. Steadman, K. Reese, R. Walker, S. Conant, and one anonymous reviewer for their comments. SLP thanks the Pew Fellowship in Conservation and the Environment for support.