

## DISTRIBUTIONS OF NEW ZEALAND BIRDS ON REAL AND VIRTUAL ISLANDS

**Summary:** This paper considers how habitat geometry affects New Zealand bird distributions on land-bridge islands, oceanic islands, and forest patches. The data base consists of distributions of 60 native land and freshwater bird species on 31 islands. A theoretical section examines how species incidences should vary with factors such as population density, island area, and dispersal ability, in two cases: immigration possible or impossible. New Zealand bird species are divided into water-crossers and non-crossers on the basis of six types of evidence. Overwater colonists of New Zealand from Australia tend to evolve into non-crossers through becoming flightless or else acquiring a fear of flying over water. The number of land-bridge islands occupied per species increases with abundance and is greater for water-crossers than for non-crossers, as expected theoretically. Non-crossers are virtually restricted to large land-bridge islands. The ability to occupy small islands correlates with abundance. Some absences of species from particular islands are due to man-caused extinctions, unfulfilled habitat requirements, or lack of foster hosts. However, many absences have no such explanation and simply represent extinctions that could not be (or have not yet been) reversed by immigrations. Extinctions of native forest species due to forest fragmentation on Banks Peninsula have especially befallen non-crossers, uncommon species, and species with large area requirements. In forest fragments throughout New Zealand the distributions and area requirements of species reflect their population density and dispersal ability. All these patterns make abundantly clear that the future of New Zealand bird species confined to native forest hinges on preserving large tracts of native forest.

**Keywords:** Island biogeography; avian biogeography; biogeography; island avifauna; avifauna; oceanic islands; forest patches; land-bridge islands; reserves; conservation; Banks Peninsula; New Zealand.

### Introduction

During the past two decades one of the most active areas of biogeography has focused on studying how the geometry of available habitat affects species distributions. This field was rekindled by the book of MacArthur and Wilson (1967), and a recent issue of *Oikos* (Bengtson and Enckell, 1983) illustrates the present diversity of approaches. The discipline is commonly termed island biogeography, since real islands, with their sharp boundaries, have proved especially convenient for studying influences of geometry.

Actually, distributions of many other habitats besides islands resemble archipelagoes, in that the habitat occurs in patches surrounded by terrain as alien to species of the habitat as is the ocean to terrestrial species. Examples include forest patches surrounded by farmland, alpine summits surrounded by forest, and lakes and rivers surrounded by land of any sort. Understanding of species distributions in discrete habitat patches may serve as a stepping-stone towards solving more complicated problems of distributions in continuous expanses of continental habitats (Cody, 1975). Island biogeography has also become of practical importance to conservation biologists, with the recognition that island studies offer useful models for predicting the fates of isolated populations in nature reserves surrounded by man-modified habitats (Willis, 1974; Wilson

and Willis, 1975; Terborgh, 1974, 1975; Diamond, 1975a, 1976a; Fleming, 1975; Dawson and Hackwell, 1978).

At least three reasons make New Zealand a fertile ground for island biogeographic studies. New Zealand is itself an oceanic island; it consists of an archipelago of islands of varying areas, isolations, and geological histories; and the future of much of its battered biota hinges on forest reserves of varying sizes and degrees of isolation. Gordon Williams pioneered the application of modern island biogeographic methods to understanding bird, insect, and plant distributions in the New Zealand region (Williams, 1981, 1982). My own interests in New Zealand grew out of my studies of the related avifauna of New Guinea, and developed during three visits that I made to New Zealand to census birds in 1966, 1968, and 1979. During Gordon's sabbatical visit to Los Angeles in February 1983 he and I laid the foundations of what we planned to be a collaborative biogeographic study of New Zealand birds. The present paper springs from those discussions and is dedicated to Gordon's memory.

In this paper I examine the effect of habitat geometry on distributions of New Zealand's native land and freshwater birds in four island-like situations: land-bridge islands, oceanic islands, forest fragments of Banks Peninsula, and

forest fragments of New Zealand generally. I introduce these analyses with a theoretical discussion of how island geometry is likely to affect species distributions. The paper concludes by mentioning implications of this material for avian conservation in New Zealand.

## Theory

Why should species distributions depend on island area and isolation? To answer this question, it is convenient to distinguish two situations, depending upon whether or not immigration to islands is possible.

### *Case 1. No immigration possible.*

In one idealized situation suppose that islands somehow started out with a set of species but that no species can arrive thereafter, and that a population which goes extinct cannot be restored by immigrants. An actual situation approaching this ideal consists of populations of species unable to cross water (e.g. kiwis<sup>1</sup>, saddleback) on land-bridge islands that were connected to North or South Island until late-Pleistocene rising sea levels sundered the land bridges (e.g., Stewart, Great Barrier). Another example involves populations of flightless forest bird species on mainland forest patches that were formerly part of continuous forest but that are now widely separated by open country. In each case the islands start off with a set of species, and lose species irreversibly as populations become extinct (Diamond, 1972; Terborgh, 1974).

Since we assume immigration to be impossible, the only process modifying species distributions from the initial state is extinction. Events such as habitat destruction and other catastrophes can exterminate species indiscriminately, while hunting or introduction of disease or predators can exterminate species selectively for reasons particular to each species. What if there is no such catastrophe or selective cause of extinction, but just fluctuations of populations in response to their internal dynamics and to climatic fluctuations? A host of case studies that I reviewed elsewhere (Diamond, 1984) shows that the most important predictor of extinctions in a fluctuating environment is small population size. Other predictors include short generation time, colonial breeding, low ratio or small difference

between birth and death rates, and high year-to-year variability in numbers.

These conclusions may be expressed by writing

$$E_{ij} = e_i / N_{ij}^{x_i} = e_i / (\bar{\rho}_i A_j)^{x_i} \quad (\text{eq. 1})$$

Where  $E_{ij}$  = probability per unit time that species  $i$  will go extinct on island  $j$ ;  
 $N_{ij}$  = time-averaged population size of species  $i$  on island  $j$ ;  
 $\bar{\rho}_i$  = population density of species  $i$  (pairs per km<sup>2</sup>);  
 $A_j$  = area of island  $j$ ;  
 $x_i$  = a species-specific exponent, close to 1 in some studies (Gilpin and Diamond, 1976);  
 $e_i$  = a species-specific constant that depends on generation time, year-to-year variability in numbers, etc.

In this simplified discussion we pretend that islands differ only in area. Deviations from this assumption will tend to cause  $e_i$ ,  $\bar{\rho}_i$ , and possibly  $x_i$  to vary among islands as well as among species.

Reasons for a low population density,  $\bar{\rho}_i$ , may be either that most of the island's habitat is suitable but that the species requires a large territory; or else that the species has specialized habitat requirements satisfied by only a small fraction of the island's area.

We may express the probability that species  $i$  is still present on island  $j$  after time  $t$  as  $J_{ij}(t)$ . Alternatively, if we take a group of identical islands all starting out with species  $i$  present,  $J_{ij}(t)$  is the fraction of islands still supporting species  $i$  after time  $t$ . For this case in which immigration is assumed impossible,  $J_{ij}(t)$ , termed the incidence of species  $i$  (Diamond, 1975b), is simply given by

$$J_{ij}(t) = e^{-E_{ij}t} \quad (\text{eq.2})$$

where  $E_{ij}$  is in turn given by eq. 1, and  $e$  is the base of natural logarithms.

Figure 1 illustrates graphs of  $J_{ij}$  against  $t$ , for a common, uncommon, and rare species on a large or a small island. Figure 2 plots  $J_{ij}$  against  $A_j$  for several choices of  $t$ . These figures yield the following conclusions:

1. As time passes, populations will gradually go extinct.
2. On a given island a rare species will tend to go extinct sooner than a common species.
3. A given species will tend to go extinct sooner on a small island than on a large island.

<sup>1</sup> Refer to Table 2 for scientific names.

Incidence vs. time, at different population densities  
Case I: no immigration possible

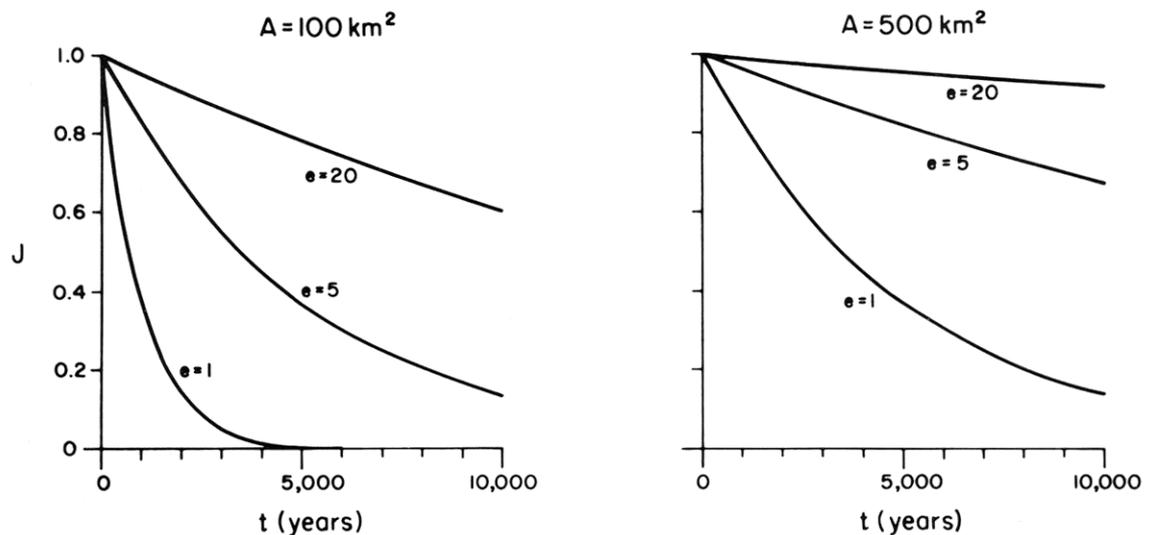


Figure 1: Incidence ( $J$ , ordinate) as a function of time (abscissa), for a land-bridge island of area  $100 \text{ km}^2$  (left) or  $500 \text{ km}^2$  (right), in the case where extinctions are irreversible because immigration is impossible. Land-bridge islands are assumed to start out with a certain quota of species. At  $t = 0$  the land-bridges are severed, and  $J$  decreases as populations go extinct.  $J$  is calculated from eqs. 1 and 2, with  $e_i = 0.1$  per year,  $x_i = 1$ , and  $e_i = 1, 5, \text{ or } 20$  pairs per  $\text{km}^2$ . Note that  $J$  decreases more slowly for denser populations and on the larger islands.

4. At a given time the species composition of smaller islands will tend to be nested subsets of those of larger islands.

It is worth reiterating the "Simplifying assumptions of this model that might cause it to be a poor description of actual species distributions. The main such assumptions are that:

1. All islands start off with the same set of species<sup>2</sup>;
2. Immigration is impossible after the islands have become isolated;
3. Populations are not exterminated by wholesale catastrophes or selective agents;
4. Island differences in factors other than area are of minor importance;
5. Species differences in population size are the main cause of species difference in proneness to extinction.

Obviously, one or more of these assumptions could prove invalid in a given situation. I introduce the model, not because I think it is literally true, but because its failures will help us

2. In fact, if one compares different-sized patches of a mainland, larger patches will be found to support more species. This relation is termed the continental species / area relation and can often be described by an equation of the form  $S = S_0 A^z$ , where  $z$  is lower than for comparisons of species number on different-sized islands (MacArthur and Wilson, 1967). For instance,  $z = 0.055$  for the New Guinea mainland,  $0.22$  for oceanic islands near New Guinea (Diamond and Gilpin, 1983). Thus, part of the reason why large land-bridge islands have more species than small ones is that the larger islands started off with more species. However, the low  $z$  value for mainland patches means that this effect is qualitatively less important than the fact that at a given time after isolation a small land-bridge island will have lost a greater fraction of its initial species set than will a larger island.

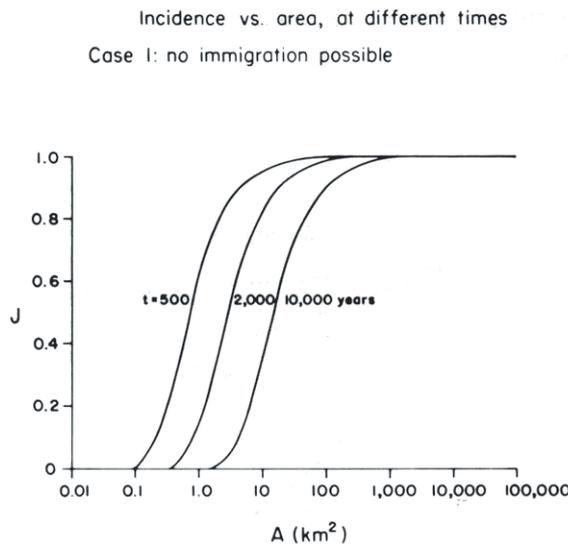


Figure 2: Incidence (*J*, ordinate) as a function of area (abscissa: logarithmic scale) for land-bridge islands, at 500, 2,000, or 10,000 years after the bridges are severed. Immigration is assumed impossible, so that extinctions are irreversible. *J* is calculated from eqs. 1 and 2, with  $e_i = 0.1$  per year,  $x_i = 1$ , and  $l_i = 100$  pairs per  $km^2$ . Note that *J* increases with area and decreases with time.

to identify other factors beside these first obvious ones and thus to construct more realistic models.

*Case 2. Immigration possible.*

In the opposite idealized extreme situation, we assume that an extinct population can be restored by immigrants. If we observe a particular island (say; island *j*) for a long time, we will find that a particular species (say, species *i*) may be present for a while and then may disappear for a while until immigrants restore the population. As in the previous case, we use *J<sub>ij</sub>* to symbolize the probability that we will find species *i* on island *j* at any instant. However, since (in contrast with Case 1) we postulate a steady state, *J<sub>ij</sub>* now also means the fraction of total time that species *i* will be present on the island. Alternatively, if we have many identical islands and wait until the system is in a steady state, *J<sub>ij</sub>* symbolizes the fraction of all islands that at a given instant will be found to support species *i*.

Consider this steady-state situation, where the fraction of inhabited islands *J<sub>ij</sub>* is no longer

changing with time, because the rate of immigration of species *i* to islands lacking the species (*I<sub>ij</sub>* times 1-*J*) equals the rate of extinction on islands having the species (*E<sub>ij</sub>* times *J*). In this steady-state the incidence *J<sub>ij</sub>* is simply obtained by solving  $I_{ij}(1-J) = E_{ij}J$ , to yield

$$J_{ij} = I_{ij}/(E_{ij} + I_{ij}) \tag{eq. 3}$$

We already discussed *E<sub>ij</sub>* in connections with Case 1. What determines *I<sub>ij</sub>*, the probability of immigration per unit time? At least six factors can be identified: three specific to species *i*, two to island *j*, and one to the source region.

First, the number of immigrants will be proportional to the size of species *i*'s population in the source region, *N<sub>is</sub>* (where *s* refers to source), in turn equal to the source's area *A<sub>s</sub>* times the species' population density (*i*). Next, the rate at which immigrants leave the source varies greatly among species and may be expressed by a proportionality constant *c<sub>i</sub>* (high for wanderers like tui, low for long-lived sedentary species like kea). The distance that an immigrant is likely to fly also varies greatly among species and may be expressed by a "space constant" *D<sub>i</sub>* (high for grey teal and grey duck, low for saddleback and kokako). As for the target island, the number of immigrants that it intercepts will increase with its area *A<sub>i</sub>* and will decrease with its distance *D<sub>j</sub>*. The likelihood that an immigrant will find suitable habitat on an island also increases with its area *A<sub>j</sub>*. Other studies (Gilpin and Diamond, 1976) suggest that a satisfactory expression for immigration is obtained by combining these factors in the form

$$I_{ij} = \zeta_i A_s c_i A_j e^{-y D_j / D_i} \tag{eq. 4}$$

where  $y < 1$ . (If  $y = 0$ , then  $A_j = 1$  and the effect of target area is negligible). This expression states that the probability of immigration is proportional to the source population size ( $\zeta_i A_s$  and to some power of the target island area *A<sub>j</sub>*, and falls off exponentially with distance *D<sub>j</sub>* according to a species-specific space constant *D<sub>i</sub>*.

*J<sub>ij</sub>* is calculated by substituting eqs. 1 and 4 into eq. 3 (d. Diamond and Marshall, 1977). Figure 3 plots *J<sub>ij</sub>* vs. *A<sub>j</sub>* for various ratios of *c<sub>i</sub>* to *e<sub>i</sub>*. It will be seen that Incidence increases steeply with island area *A<sub>j</sub>*. However, the area for which an island has a 50% chance of being occupied by the species (abbreviated *A<sub>0.5</sub>*) varies greatly among species, depending on their relative values of *c<sub>i</sub>* and *e<sub>i</sub>*. *A<sub>0.5</sub>* may be thought of as

approximately a critical island area or patch size below which one is increasingly unlikely to find the species.

Eq. 3 yields the following conclusions:

1. For a given species, incidence increases with island area because of decreased risk of extinction, and also because of increased likelihood of immigration.

Incidence vs. area  
Case 2: immigration possible

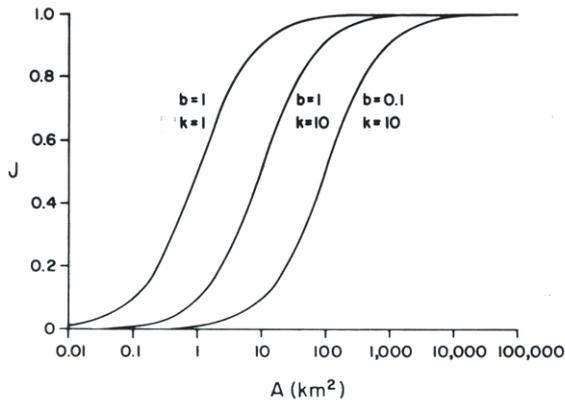


Figure 3: Incidence ( $J$ , ordinate) as a function of island area (abscissa: logarithmic scale) in the steady state where incidence is unchanging because populations are immigrating as often as going extinct.  $J$  is calculated from eqs. 1, 3, and 4, with  $x_i = 1$ ,  $e_i/q_i \equiv k = 1$  or  $10$ ,  $y = 0$ ,  $q_i A_s c_i e^{-D_j/D_i} \equiv b = 1$  or  $0.1$ .

2. For a given species, incidence decreases with distance because of decreased immigration (also because of increased extinction, as a population on the verge of extinction is less likely to be saved by immigrants: the rescue effect of Brown and Kodric-Brown (1977)).

3. For a given island area, incidence is higher for common species (high  $l_i$ ) than for rare species, both because of lower risk of extinction and higher likelihood of immigration (more colonists leaving the source).

4. For a given island area, incidence is higher for a species prone to disperse (high  $c_i$ ) than for a

sedentary species. Note, however, that the relevant dispersal is not that between wintering and summering grounds but instead that between natal site and breeding site (or else between successive breeding sites). A species of which individuals disperse only once in their lives (as juveniles) and then remain sedentary counts as an effective disperser (e.g., tomtit). A species that migrates long distances every year between summer and winter quarters but returns to the same breeding site counts as a poor disperser (e.g., some long-distance migrants in North America: Diamond and Jones, 1980).

5. Distant islands will tend to be occupied preferentially by species that are long-distance dispersers (high  $D_i$ ).

As in case 1, I reiterate that the model contains simplifying assumptions and is not believed to be literally true. For example, rather than a single source of area  $A_s$  concentrated at distance  $D_j$ , a more complicated but realistic model would integrate source areas over their distances. Note also that cases 1 and 2 represent opposite extremes of a spectrum: no immigration, or else immigration in a steady-state world. Many situations may fall between these extremes: a pulse of dispersal followed by a period of no dispersal in response to altered climate or habitat. Finally, note that Figures 2 and 3 both show incidence as increasing with island area, whether or not immigration is possible. Thus, one cannot determine whether island populations are over-water colonists or land-bridge relicts merely by examining the area dependence of incidence.

### Bird Distributions on Land-bridge Islands

Today, New Zealand is an archipelago of two large islands and dozens of small ones. However, at Pleistocene times of low sea level most of these islands were joined into a single giant island, which we shall term "Greater New Zealand". The modern fragments of this Pleistocene giant island are called land-bridge islands (mainland and offshore islands in the terminology of Williams, 1981), while islands that are surrounded by deep water and that consequently were never part of Greater New Zealand are termed oceanic islands (or outlying islands: Williams, 1981). Table 1 divides 31 islands of the New Zealand region into these two classes and lists for each island the area, the distance from North or South or Stewart Islands, and the number of native resident land or freshwater bird species.

Table 1: *Land-bridge and oceanic islands of the New Zealand region.*

Island or island group	Area (km <sup>2</sup> )	Distance (km)	Number of resident species	% non-crossers
<i>land-bridge islands</i>				
1. South	150,000	—	50	44
2. North	114,700	—	47	40
3. Stewart	1,735	—	34	26
4. Great Barrier	300	19	29	17
5. D'Urville	162	0.5	32	31
6. Little Barrier	30	22	20	20
7. Mercury	22	8	11	0
8. Kapiti	20	5	18	6
9. Codfish	15	3	18	11
10. Mayor	13	27	12	8
11. Big South Cape	8	3	13	15
12. Hen	7.2	18	14	7
13. Cavalli	4	3	8	0
14. Great King	3.5	53	11	0
15. Chetwode	3.2	3	14	0
16. Chicken	3.1	10	8	0
17. Poor Knights	2.1	22	7	0
18. Cuvier	1.9	25	7	14
19. Stephens	1.5	24	9-23	22(?)
20. Solander	1.4	37	6	0
21. Whale	1.4	11	5	0
22. Aldermen	0.9	20	8	0
<i>oceanic islands</i>				
23. Chatham	909	645	26	—
24. Auckland	464	370	11	—
25. Campbell	114	590	4	—
26. Macquarie	100	1,100	3	—
27. Norfolk	34.5	750	18	—
28. Raoul	31	975	7	—
29. Antipodes	20.7	730	3	—
30. Lord Howe	14	1,300	17	—
31. Snares	2.8	105	2	—

Data are from Williams (1981), with the following exceptions: White Island is omitted because it is an active volcano; the islands are renumbered; and the number of species for Norfolk and Lord Howe are extracted from Hindwood (1940), Hindwood and Cunningham (1950), McKean and Hindwood (1965), Greenway (1967), and Recher (1974). Distance is taken from North, South, or Stewart Islands. Number of resident species refers only to the native land and freshwater bird species listed in Table 2. The last column (land-bridge islands only) gives the percentage of species on the island that are non-crossers of water gaps (identified by N in Table 2).

Table 2 gives details of island distributions for the 60 native resident land and freshwater bird species of the New Zealand region. For the purposes of the following analysis the whitehead/yellowhead superspecies, grey warbler/Chatham Island warbler superspecies, and robin/Chatham Island robin superspecies are each analyzed as a unit, yielding 57 "zoogeographical species" in the sense of Mayr and Short (1970).

#### *Water-crossing vs. non-crossing species.*

Of the 57 zoogeographical species of Table 2, 31 (denoted by X in column 1 of Table 2) are resident on one or more oceanic islands which they could only have reached by flying overwater. Three (the two flightless rails of the Chathams plus the Antipodes Island parakeet, denoted by (N) in column 1) are confined to single oceanic islands or groups, and 23 (denoted by N in column 1) are confined to land-bridge islands.

Table 2: Native land and freshwater bird species of the New Zealand region. Column 1: N = non-crosser confined to land-bridge islands, (N) = non-crosser endemic to one oceanic island or island group, X = water-crosser. Column 3: 0 = order, F = family, G = genus, S = full species, A = allospecies, sub = subspecies endemic to New Zealand region; — = New Zealand and Australian populations belong to same subspecies. Columns 4 and 5: land-bridge and oceanic islands respectively on which the species is resident, identified by the island numbers in Table 1. Column 6: five types of evidence for water-crossing ability besides presence as resident on oceanic island of New Zealand region; Au = resident in Australia; str = recorded as vagrant on a New Zealand island; mig = long-distance overwater migrant; Pac = resident on a remote Pacific island; As = resident on an Indonesian island, Eurasia, or Africa. Column 7: total number of land-bridge islands occupied. Column 8: population density, categorized as low, medium, or high. Column 9: area range of land-bridge islands for which the species' incidence drops to 0.5.

column 1	2	3	4	5	6	7	8	9
water-crosser?	species	endemism	land-bridge	oceanic	water crossing evidence	number of l.-b. islands	abundance	$A_{0.5}$ (km <sup>2</sup> )
N	Brown kiwi	0	1-3	—	—	3	low	>1,000
N	Little spotted kiwi	0	1,2,5	—	—	3	low	>100
N	Great spotted kiwi	0	1	—	—	1	low	>100
X	Crested grebe	—	1,2	—	Au,As	2	—	—
N	Dabchick	A	1,2	—	—	2	—	—
X	Paradise shelduck	S	1,2,5	23	str	3	—	—
X	Grey teal	—	1,2	—	Au, str, Pac, As	2	—	—
X	Brown teal	S	1-4,6	23-25	As	5	—	—
X	Grey duck	sub	1-5,8,10	23-26,28	str	7	—	—
X	Shoveler	sub	1,2	23	Au, str, Pac, As	2	—	—
N	Blue duck	G	1,2	—	—	2	—	—
N	Scaup	S	1,2,5,10	—	—	4	—	—
X	Harrier	—	1-5,7,9,13,15,17,19,21	23	Au, str, Pac	12	low	1-10
X	Falcon	S	1-5,19	23,24	str	6	low	10-100
X	Quail	sub	1,2	—	Au	2	—	—
X	Banded rail	sub	1-4,6,14,17,19	23,26	Au, Pac, As	8	—	—
(N)	Dieffenbach's rail	A	—	23	—	—	—	—
X	Auckland Island rail	sub	—	24	Au, As	—	—	—
(N)	Chatham Island rail	S	—	23	—	—	—	—
N	Weka	S	1-3,5	—	—	4	med	>100
X	Marsh crake	sub	1-3	23	Au, As	3	—	—
X	Spotless crake	—	1-5,14,17	23,28	Au, Pac	7	—	—
X	Pukeko	—	1-5,7	23,28,30	Au, str, Pac, As	6	—	—
N	Takahe	S	1,2	—	—	2	low	>1,000
X	Pigeon	G	1-10,12,15,16,18,19	23,27	—	15	med	1-10
N	Kakapo	G	1-3	—	—	3	low	>1,000
X	Kaka	G	1-6,8-10,12,15,19	23,27	str	12	low	1-10

Table 2: Native land and freshwater bird species of the New Zealand region. (Continued)

column 1	2	3	4	5	6	7	8	9	
water-crosser?	species	endemism	land-bridge	Islands	oceanic	water crossing evidence	number of l.-b. islands	abundance	$A_{0.5}$ (km <sup>2</sup> )
N	Kea		1	—	—	—	1	low	>1,000
(N)	Antipodes Island parakeet	G	—	29	—	—	—	—	—
X	Red-crowned parakeet	S	1-9,11,12,14,17,22	23,24,26-30	Pac	—	14	med	1-10
X	Yellow-crowned parakeet	S	1-6,8,9,11,12,15,19,20	23,24,	str	—	13	med	1-10
N	Orange-fronted parakeet	S	1	—	—	—	1	low	>1,000
X	Shining cuckoo	sub	1-6,8-10,12,15,19	23,27	Au,mig,Pac	—	12	med	1-10
X	Long-tailed cuckoo	S	1-5,8,9,19	28	mig	—	8	low	10-100
X	Morepork	sub	1-12,14-16,19,21	27,30	Au,As	—	17	med	1-10
N	Laughing owl	G	1-3	—	—	—	3	low	>1,000
X	Kingfisher	sub	1-10,12-15,17-19,21,22	27-30	Au,Pac	—	19	med	1-10
N	Rifleman	F	1-6,9,20	—	—	—	8	high	10-100
N	Bush wren	F	1-3,11	—	—	—	4	med	>100
N	Rock wren	F	1	—	—	—	1	—	—
N	Stephens Island wren	F	19	—	—	—	1	—	—
X	Pipit	sub	1-5,7,8,13-15,17,19,22	23-25,29	Au,str,As	—	13	—	—
X	Fernbird	G	1-5,9,11,14,19,22	23,31	—	—	10	—	—
N	Brown creeper	G	1,3,5,9	—	—	—	4	med	10-100
N	Whitehead	G	2,4,6,8	—	—	—	6	high	10-100
	Yellowhead		1,5	—	—	—	—	—	—
	Grey warbler		1,16,18,20-22	27,30	—	—	—	—	—
X	Chatham Island warbler	S	—	23	—	—	20	high	<1
X	Fantail	sub	1-16,18-22	23,30	—	—	21	high	<1
X	Tomtit	S	1-6,8,9,11,12,16,19,20	23,24,31	Au,Pac	—	13	high	1-10
X	Robin	S	1-6,8,11,15,19	23	—	—	10	med	10-100
	Chatham Island robin		—	—	—	—	—	—	—
X	Silvereye	—	1-13,15,18-20,22	23-25,27,30	Au,str,Pac	—	18	high	<1

Table 2: Native land and freshwater bird species of the New Zealand region. (Continued)

column 1	2	3	4	5	6	7	8	9	
water-crosser?	species	endemism	land-bridge	Islands	oceanic	water crossing evidence	number of l.-b. islands	abundance	$A_{0.5}$ (km <sup>2</sup> )
N	Stitchbird	G	2,4,6	—	—	—	3	high	10–100
X	Bellbird	G	1–20,22	23,24	—	—	21	high	<1
X	Tui	G	1–6,8–16,	23,24,28	—	str	16	high	1–10
	<i>noavaeseelandiae</i>								
N	Saddleback	F	1–6,9,11,12,19	—	—	—	10	high	10–100
	<i>carunculatus</i>								
N	Huia	F	2	—	—	—	1	low	>1,000
N	Kokako	F	1–5,19	—	—	—	6	low	10–100
N	Piopio	F	1,2,5,19	—	—	—	4	med	10–100
	<i>Turnagra capensis</i>								

Thus, as recognized by Williams (1981), 31 species have, by this criterion, evinced ability to cross water, while 26 have not.

One might object to this distinction between water-crossers and non-crossers on the grounds that the New Zealand region has only nine oceanic islands available for inclusion in Tables 1 and 2, and some of these islands have few species. Thus, even if all species were distributed over land-bridge and oceanic islands at random, some species by chance would appear to be confined to land-bridge islands. In fact, for 25 of the 31 species labelled as water-crossers there are up to five types of other evidence for water-crossing ability (indicated in column 6 of Table 2) besides residence on one or more oceanic islands of the New Zealand region. These five types of evidence are: annual overwater migration of the New Zealand population to remote Pacific islands (the two cuckoos); overwater straggling (records especially extensive for Little Barrier (Hamilton, 1961) and Lord Howe) or regular commuting to islands on which the species is not resident (13 species); presence on the opposite side of the Tasman Sea in Australia (17 species); presence on remote Pacific islands such as New Hebrides, New Caledonia, Fiji, Samoa, Tahiti, and Marquesas (11 species); and presence in Indonesia, Asia, or even Europe and Africa (nine species). The 23 species confined to land-bridge islands have not only failed to reach any of the nine oceanic islands but have also failed to evince any of these other five proofs of water-crossing ability. Thus, their confinement to the land-bridge islands is not a distributional accident but really indicates deficient water-crossing ability.

More detailed studies would be needed to determine just how wide a water gap is required to stop the "non-crossers". Presumably most of them would cross 1 m of water, but would they cross 10 m? 500 m? 5 km? My guess is that within historic times none of them has crossed a 5 km strait, and few if any have crossed a 500 m strait. However, the saddleback has crossed a 250 m strait (Newman, 1980).

Could one predict failure to cross water gaps just by observing a bird's behaviour? Of the 23 non-crossers, six are flightless (three kiwis, weka, takahe, and kakapo), and eight fly weakly or only short distances (four New Zealand wrens, three callaeids, and piopio). These 14 species may be mechanically incapable of crossing broad water gaps. The remaining nine species (dabchick, scaup, blue duck, kea, orange-fronted parakeet,

laughing owl, brown creeper, whitehead/yellowhead, stitch bird) are normal or strong fliers. Some of them, especially the kea, dabchick, and scaup can be seen to fly distances overland exceeding the width of numerous straits that the species has never been known to cross. These species must be non-crossers for behavioural reasons: they are afflicted with a fear of flying overwater Uong, 1973; Diamond, 1981). The tropics provide many more examples of species that are powerful fliers overland, such as swifts and eagles, but that refuse to cross even narrow water gaps (Diamond, 1976a; Diamond and Gilpin, 1983).

Among the 31 water-crossers too, observations of behaviour are an imperfect guide to colonizing ability. Some fly a lot in the course of their daily foraging (e.g., harrier, falcon, kaka, red- and yellow-crowned parakeets), and some wander seasonally (e.g., tui). However, others are sedentary, have small territories, and do not make long foraging flights (e.g., tomtit, robin, warbler, morepork, kingfisher). Probably the latter five species disperse overwater mainly as juveniles in search of a territory, then remain sedentary. The fernbird, pukeko, banded rail, and two crakes normally give the appearance of being weak fliers, but the rails are visibly strong fliers once airborne.

Thus, possessing the necessary strength of flight is a necessary but not sufficient condition, and flying long distances overland on a daily basis is not even a necessary condition for overwater dispersal ability. In addition to possession of the necessary mechanical equipment, overwater dispersal requires a specific behavioural component that is subject to natural selection. While the ancestors of some of the non-crossers, such as the New Zealand wrens (Sibley, Williams and Ahlquist, 1982), may have reached New Zealand overland 100 million years ago when it was part of Gondwanaland, others must have arrived more recently overwater and subsequently lost their mechanical or behavioural adaptations for water-crossing. Taxa that became mechanically flightless after reaching New Zealand or its oceanic islands include the takahe, Auckland Island teal, Dieffenbach's rail, Chatham Island rail, and weka, derived from ancestors similar to the volant pukeko, brown teal, banded rail, banded rail, and banded rail, respectively. Taxa that became behaviourally flightless overwater include dabchick and scaup, derived from ancestors that arrived overwater from

Australia, where they are still represented by the hoary-headed grebe (*Podiceps poliocephalus*) and white-eyed duck (*Aythya australis*), respectively.

Table 3 shows that the percentage of water-crossers decreases with increasingly high levels of endemism among New Zealand bird species. Of course, the non-endemic taxa and the taxa endemic only at the subspecies level are all water-crossers by definition. However, there is no such tautology to explain why only half of New Zealand's endemic allospecies, species, and members of endemic genera, and no members of endemic families or orders, occur on islands lacking Pleistocene land bridges to New Zealand<sup>3</sup>. The absences on oceanic islands are surprising especially because the old endemics are the species that have had the longest time to reach outlying islands, and one might therefore have expected them to be disproportionately well represented there. In reality, the outlying islands are mainly occupied by taxa whose conspecifics or congeners can still be recognized across the Tasman Sea in Australia.

This pattern suggests that species arriving from Australia tend to reach both New Zealand and the outlying islands in their first colonization wave, as observed for the silvereye since its arrival in the 19th century. As the colonists adapt with time to the New Zealand region and become endemic taxa, selection operates against overwater dispersal ability, and extinctions of populations on small outlying islands can no longer be reversed by new colonists from New Zealand. This reconstructed evolutionary history of New Zealand's avifauna is similar to the taxon cycle by which sedentary endemic arthropod species on many Pacific islands evolved from vagile ancestors, according to Wilson (1961).

<sup>3</sup> One could object that a taxon that retained its water-crossing ability would be likely to colonize islands beyond the New Zealand region, causing it to be considered non-endemic and making the reasoning circular. In fact, on other Pacific Islands the only modern taxa apparently derived from New Zealand ancestors are the two extinct *Cyanorhamphus* parakeets of the Society Islands and the race of the red-crowned parakeet on New Caledonia. In Table 2 I ignore the laner race and still consider the red-crowned parakeet a species endemic to the New Zealand region. If one considered New Zealand's four parakeets as members of endemic genera rather than endemic species, on the grounds that the genus had arisen in New Zealand and then spread elsewhere, the conclusions of this section would not be qualitatively altered.

Table 3: *Water-crossing ability as a function of level of endemism.*

Level of endemism	Total number of species	Number of water-crossing species	Number of non-crossing species	Percentage of species that are water-crossers
Non-endemic	6	6	0	100
Endemic subspecies	11	11	0	100
Endemic allospecies or full species	17	9	8	52
Endemic genus	12	5	7	42
Endemic family	8	0	8	0
Endemic order	3	0	3	0

All 57 New Zealand native land and freshwater bird species are grouped in column 1 by their level of endemism (from column 3 of Table 2). Column 4 gives the number of species that do not cross water (denoted N or (N) in column 1 of Table 2); column 3, the number of water-crossers (denoted X in column 1 of Table 2); column 5, the percentage of water-crossers (column 3 as a percentage of column 2). Note that water-crossing ability decreases with level of endemism, suggesting selection against water crossing ability in New Zealand birds.

#### *Islands per species*

The theory section made predictions about how a species' distribution should be determined by such biological characteristics as its abundance and dispersal ability. A simple test of these predictions is to calculate the number of islands that a species inhabits. All other things being equal, this number should increase with abundance and dispersal ability.

We already know that non-crossing species are absent from a whole group of islands, the oceanic islands. Let us therefore confine our comparisons to the 22 land-bridge islands, the only ones on which non-crossing as well as water-crossing species have any possibility of occurring. Furthermore, some species are confined to habitats such as fresh water, swamps, and cleared land, which occur only on certain islands in idiosyncratic fashion. Let us therefore omit from our analysis the species of these habitats (all ducks and grebes, all rails except weka and takahe, plus quail, pipit, fernbird, and rock wren). I also omit the very localized Antipodes Islands parakeet and the poorly known Stephens Island wren. This leaves us with 18 non-crossing and 17 water-crossing species for further analysis. Column 7 of Table 2 gives the number of land-bridge islands occupied by each species.

The 18 non-crossers occupy on the average  $3.7 \pm 2.5$  land-bridge islands (mean  $\pm$  S. D.), the 17 water-crossers  $14.5 \pm 4.4$  land-bridge islands (Table 4). Thus, the average water-crosser occupies four times as many islands as the average non-crosser. The simplest explanation, and the one which I believe to be the most important factor, is that the water-crossers have the means to reoccupy an island after a population has gone

extinct for any reason, while the non-crossers lack this means. I consider additional possible contributing factors below.

Column 8 of Table 2 categorizes the population densities of these 35 species in three categories: low, medium, and high abundance. For extant species these decisions are based on censuses that I carried out in the 1968 breeding season for nine North Island native forest sites in Urewera and Tongariro National Parks, and 28 South Island native forest sites in Arthur's Pass, Westland, and Fiordland National Parks, plus a 1979 census in Little Barrier Island forest. These censuses are supplemented by published censuses on South Island and Little Barrier Island by Kikkawa (1964, 1966), in North Westland by Crook, Best, and Harrison (1977), and in Whirinaki State Forest by Moynihan, Imboden, and Ogle (1979). For species now extinct or virtually so, I relied on older literature. It is obvious that population densities vary locally and that these categorizations are very crude, but they should suffice for a first test of whether even crude measures of abundance can help explain distributions. As examples of the three categories, I consider kiwis, harrier, falcon, kaka, long-tailed cuckoo, laughing owl, and huia to have (or to have had) low population density; weka, pigeon, red- and yellow-crowned parakeets, robin, and brown creeper, medium population density; and rifleman, grey warbler, whitehead/yellowhead, tomtit, and the three honey-eaters, high population density.

Table 4 shows that, both for water-crossers and non-crossers, the number of islands occupied increases with population density. At any level of abundance, the number is greater for water

Table 4: *Islands per species*

	Population density			All species
	Low	Medium	High	
Water-crossers	9.5 ± 3.0 (4)	14.3 ± 3.0 (7)	18.2 ± 3.2 (6)	14.5 ± 4.4 (17)
Non-crossers	2.4 ± 1.6 (10)	4.0 ± 0.0 (4)	6.8 ± 3.0 (4)	3.7 ± 2.5 (18)

The number of land-bridge islands occupied is tabulated for 18 of the 23 non-crossers and 17 of the 31 water-crossers (respectively N and X in column 1 of Table 2), after excluding species of specialized habitats as described in the text. Each group of species is then subdivided by population density, as indicated in column 8 of Table 2 and as discussed in the text. Note that water-crossers occupy more islands than non-crossers, and that number of islands occupied increases with population density.

crossers than for non-crossers. For the non-crossers there is a single reason why number of islands correlates with population density; the larger the species' population on an island, the less likely is the population to go extinct. For water-crossers this reason still applies, plus another reason as well; abundant species send out more immigrants and are more likely to reoccupy islands after an extinction.

The correlation between abundance and number of islands occupied, both for species capable and those incapable of overwater colonization, agrees with predictions in the theory section.

#### *Size of islands occupied.*

Further patterns emerge when we consider what size range of island each species occupies. Figure 4 depicts examples of incidence  $J$  as a function of island area. The form of these graphs is similar to the form of the theoretical graphs of Figures 2 and 3. From such graphs I have estimated, for the 36 species considered in Table 4, the island area  $A_{0.5}$  at which incidence drops to 0.5. These  $A_{0.5}$  values are given in column 9 of Table 2.

Of the non-crossers, most have  $A_{0.5}$  greater than 100 km<sup>2</sup>, and none has a value less than 10 km<sup>2</sup>. In fact, non-crossers are virtually restricted to islands larger than 10 km<sup>2</sup>. The exceptions are so few as to be worth detailing. Stephens Island (1.5 km<sup>2</sup>) supposedly supported, in addition to its famous wren, the rifleman, saddleback, kokako, and thrush. (Williams (1981, p. 446) questions the reliability of some early records from Stephens). Big South Cape (8 km<sup>2</sup>) had bush wren and saddleback. Hen (7.2 km<sup>2</sup>) and Cuvier (1.9 km<sup>2</sup>) have saddleback. Arid (3.9 km<sup>2</sup>) has whitehead, and Maud (2.7 km<sup>2</sup>) has rifleman (East and Williams, 1984).

The 15 species of non-crossers that occur only

on 1-3 islands are especially confined to large islands. These species are in fact confined to the five largest land-bridge islands (area 162 km<sup>2</sup>), except for the Stephens Island wren and the stitch bird population on Little Barrier. The 11 non-crossers rated as being of low abundance are confined to the three largest islands (North, South, and Stewart), except for the Stephens Island wren, the D'Urville population of little spotted kiwi, and three populations of kokako.

The virtual restriction of non-crossers, especially ones of low population density, to large

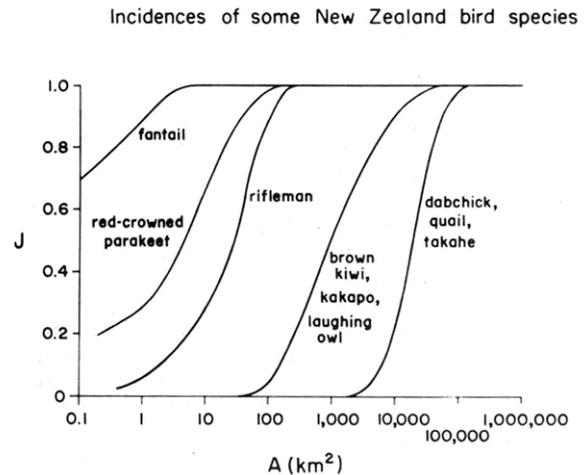


Figure 4: *Incidences of some New Zealand bird species on land-bridge islands, based on Table 2 of this paper and on some additional small islands listed in Figure 1 of East and Williams (1984). Island area is grouped into sets by area. The incidence of a species is calculated as the fraction of the sets of islands occupied by the species. Incidence is then plotted against area, and a smooth curve is drawn through the points.*

land-bridge islands is in accord with the view that most island populations of non-crossers are Pleistocene relicts, founded when the island was part of Greater New Zealand. On small islands few populations were large enough to stand much chance of surviving in the absence of immigrants for the 10 or so millenia since the land bridges were severed. A similar restriction of non-crossing species to large islands is observed for birds of New Guinea (Diamond, 1972), the neotropics (MacArthur, Diamond and Karr, 1972), and the Greater Sunda Islands (Diamond and Gilpin, 1983). Some of the "non-crosser populations" on Stephens and Big South Cape may actually have arrived overwater since the Pleistocene, since these two islands are separated by only 3 km from much larger D'Urville and Stewart Islands, respectively. Thus, with decreasing island area the percentage of species that are non-crossers decreases from 44% for South Island, the largest land-bridge island, to 0 for most islands of 4 km<sup>2</sup> or less (last column of Table 1).

The water-crossers also exhibit patterns in the size ranges of islands occupied. Most have  $A_{0.5}$  values less than 10 km<sup>2</sup>, and four (fantail, grey warbler, silvereye, bellbird) have values less than 1 km<sup>2</sup>. These values are determined partly by abundance (territory size), partly by dispersal ability, as expected from the discussion of the theory section. The four species with  $A_{0.5} < 1$  km<sup>2</sup> are all species of high abundance represented by many pairs within a 1 km<sup>2</sup> area, while two of the three species with  $A_{0.5} > 10$  km<sup>2</sup> (falcon and long-tailed cuckoo but not robin) are species of low abundance. The two most conspicuous deviations from this inverse correlation between  $A_{0.5}$  and abundance involve the two water-crossers whose dispersal ability one might guess to be the most modest: tomtit and robin. The tomtit has high abundance, but its  $A_{0.5}$  is 1-10 km<sup>2</sup>; most species of high abundance have  $A_{0.5} < 1$  km<sup>2</sup>. The robin has medium abundance but its  $A_{0.5}$  is 10-100 km<sup>2</sup>; most species of medium abundance have  $A_{0.5}$  1-10 km<sup>2</sup>.

In the extreme of very high dispersal ability, the size of island that a species can occupy should be limited only by its territory size, and one expects to find the species on islands large enough to support only one or a few pairs. It appears that this is the case for most of the 17 water-crossers for which I have tabulated  $A_{0.5}$  values. If overwater dispersal is limited, islands will remain unoccupied for a longer time after a local

population has died out, and one expects to find the species mainly on islands large enough to hold many pairs (so that local extinctions are rare). The robin and tomtit may fit this latter pattern.

#### *Reasons and "reasons" for absence of species on islands.*

Let us now consider the particular reasons why particular species might be absent on particular islands. Two major types of reasons include effects of man and habitat limitations. A minor reason, applicable only to parasitic cuckoos, is lack of suitable hosts.

In New Zealand today we are not studying an avifauna but the wreckage of an avifauna. Many species became extinct following the arrival of Maoris, and others became extinct, rare, or local following the arrival of Europeans. Olson and colleagues have emphasized the confounding effect of man-caused extinctions for island biogeographic studies (Olson and James, 1982; Steadman, Pregill and Olson, 1984). Some New Zealand bird populations vanished under the eyes of European ornithologists, such as the mainland stitch birds, saddle backs, and little spotted kiwi, and all populations of quail, laughing owl, huia, and bush wren. Other species (e.g., takahe, kakapo) were obviously contracting so rapidly in the early phase of European settlement that even the first written records show a relict distribution. The "Stephens Island wren" surely did not evolve there but rather disappeared from all other sites before ornithologists arrived. It may turn out that some cases of species absent from ecologically suitable islands are artifacts of ornithologists having been preceded by exterminating rats, cats and mustelids.

Table 4 omits consideration of water birds, swamp birds, and open-country birds (quail, fernbird, pipit) and the alpine rock wren, whose island distributions would obviously be limited by available habitat even if there were no problem of dispersal. Other species are undoubtedly also absent from certain islands because of habitat restrictions. The falcon may require cliffs as nest sites. The laughing owl may have preferred open habitats. The kea, orange-fronted parakeet, and the extant population of takahe occupy subalpine or alpine habitats, at least seasonally. Explanations of species absences from islands in terms of unfulfilled habitat requirements were carried to an extreme by Lack (1975), who virtually believed that if one could not understand why species x is absent on island y, the answer.

must lie in a habitat requirement too subtle to detect.

The island distribution of the long-tailed cuckoo matches the distributions of its principal hosts the whitehead/yellowhead and brown creeper, with two exceptions: the cuckoo does not breed on Little Barrier, where the whitehead is the most abundant bird; and the cuckoo supposedly occupies Stephens in the absence of its hosts. The shining cuckoo is absent along with its grey warbler host on Poor Knights, but the cuckoo is also absent from nine islands occupied by the warbler (Mercury, Big South Cape, Cavalli, Great King, Chicken, Cuvier, Solander, Whale, and Aldermen).

These various particular reasons undoubtedly explain some absences, but they seem to me to leave a large residue unexplained. Why does Stewart Island lack the yellow head, takahe, kea, rock wren, little spotted kiwi, great spotted kiwi, and piopio? Why did South Island lack the stitch bird and huia? Why does North Island lack the brown creeper and great spotted kiwi? Why do Kapiti, Little Barrier, Mercury, Codfish, and Mayor lack the kiwis (except as introductions), weka, takahe, kakapo, laughing owl, bush wren, kokako, and piopio? Why do Mercury and Mayor in addition lack rifleman, whitehead, tomtit, robin, and stitchbird? I suggest that anyone inclined to believe that all absences are for good reasons try the exercise of predicting species lists for each island from knowledge of island habitats and species' habitat requirements, then compare these reasonable lists with actual ones.

This is not to deny that habitat consideration and human disturbance are major factors in producing island distributions. Precisely because they are major factors, we may tend to assume that they explain everything. In fact, they leave unexplained a considerable residue of cases, for which there is no better reason than that a population went extinct because of some temporary condition, and now the species is unable, or has not yet been able, to recolonize. The main conclusion from this section is that such accidents are most likely to befall small populations (species of low abundance or populations on small islands) and species of low dispersal ability.

### Bird Distributions on Oceanic Islands

If one had species lists for large numbers of oceanic islands of various areas and at various

distances, one could calculate species incidences as a function of area and of distance, as has been done for birds of the Solomon Islands (Diamond, Gilpin and Mayr, 1976). The New Zealand region includes only nine oceanic islands, making it difficult to disentangle the effects of area and of distance. A further confounding factor is latitude, which varies from 29° to 54°30' S for the oceanic islands (Table 3 of Williams, 1981). Low latitude (29° - 31°28' S) makes Raoul, Norfolk, and Lord Howe (14 - 34.5 km<sup>2</sup>) several times richer in species (7 - 18 species), than Snares, Antipodes, Macquarie, and Campbell (2 - 4 species), which have a similar range of areas (2 - 114 km<sup>2</sup>) but lie at higher latitudes (48 - 54°30' S). Thus, the data base suffices only to note a few trends.

The tomtit is only on the two closest oceanic islands (Snares and Auckland) plus the fourth closest (Chathams); the falcon, yellow-crowned parakeet, and bellbird, only on the second and fourth closest; the brown teal, only on the second, third (Campbell), and fourth closest. The three most remote islands (Raoul, Macquarie, and Lord Howe) share the grey duck (vagrant on Lord Howe) and red-crowned parakeet. The former four species may be capable of dispersing only modest distances overwater (low  $D_i$  in eq. 4), the duck and parakeet greater distances. This conclusion is supported by the facts that the former four species have reached no islands beyond the New Zealand region, while the parakeet has reached New Caledonia and the duck has reached Pacific islands as far as Tahiti.

Of the five smallest islands (2.8 - 34.5 km<sup>2</sup>), four are occupied by the red-crowned parakeet; three, by the kingfisher; two, by the pukeko, morepork, grey warbler, and silvereye. Evidently, these species have low  $A_{0.5}$  values, as also true for their distributions on land-bridge islands, where all except pukeko have  $A_{0.5}$  values below 10 km<sup>2</sup> (column 9 of Table 2).

### Bird Distributions on Banks Peninsula

When Europeans reached New Zealand, Banks Peninsula was still forested. However, its forests were isolated from those of the rest of New Zealand by the Canterbury Plains, which had already been cleared by Maoris. Around 1840 European settlers began to cut the peninsular forests themselves. In the late 19th century much of the remaining forest was damaged by fire. Today no more than 5% of the original

peninsular forest remains, fragmented into patches of which the largest is only about 250 ha and the others 50 ha or less. Figures 3 - 5 of Johnston (1969) dramatically illustrate how the forests were greatly reduced in total area, and how the surviving forest was fragmented into small patches. The shrinkage and fragmentation of the peninsular forest by man in the late 19th century are similar to, but proceeded much faster than, the shrinkage and fragmentation of Pleistocene Greater New Zealand's forest by rising sea level around 10,000 years ago.

I have summarized elsewhere (Diamond, 1984) the peninsular avifauna, based on Turbott (1969), Potts (1873, 1874, 1882), and Gordon Williams' own observations which he discussed with me. Briefly, 19th-century ornithologists recorded 23 species of native forest birds. These did not include kea, brown kiwi, or (apart from one doubtful record) kakapo, all of which may have disappeared before recording of bird observations began. The piopio, kokako, saddleback, and probably bush wren were declining or had largely disappeared in the 1870s, around the same time that they were declining on the rest of the New Zealand mainland and presumably for the same reasons (especially introduced mammals). Eight other species (weka, falcon, red- and yellow-crowned parakeet, kaka, long-tailed cuckoo, robin, yellowhead) apparently survived till around 1900 but disappeared soon thereafter, probably mainly because of the forest shrinkage and fragmentation itself. Today only 11 native forest species (pigeon, shining cuckoo, morepork, rifleman, brown creeper, grey warbler, fantail, tomtit, bellbird, tui, silvereye), less than half the original number, still occur in peninsular forest.

Of the 19 species that survived the 1870s, why did some subsequently fare much better than others? The two correlations emerging from the list above are that species of low abundance, and species with large area requirements as judged from land-bridge islands, were the most prone to extinction in the face of forest shrinkage and fragmentation. All three species of low abundance (falcon, kaka, long-tailed cuckoo) disappeared; seven of the eight species of high abundance survived. The sole species with large area requirements on land-bridge islands ( $A_{0.5} > 100 \text{ km}^2$ ; weka) disappeared, as did four of the six species with moderate area requirements ( $A_{0.5} 10 - 100 \text{ km}^2$ ), but all four species with low area requirements (fantail, grey warbler, bell bird, silvereye:  $A_{0.5} < 1 \text{ km}^2$ )

survived. Of the seven species of medium-low area requirements ( $A_{0.5} 1 - 10 \text{ km}^2$ ) and moderate or high abundance, five survived. Thus, the same species that tended to disappear from land-bridge islands after the end of the Pleistocene tended to disappear from the shrunken and fragmented peninsular forest after European settlement.

Today, the forest holds only two non-crossing species (rifleman and brown creeper), the two others that managed to survive until the end of the century (weka and yellowhead) having subsequently disappeared. Thus, not only abundance but also dispersal ability has evidently been important to survival. The reason is that no population is likely to survive for long in a tiny patch of forest. If there are many such patches and the species can disperse between them, a temporary extinction in one patch can be reversed by colonists from another. Except in the unlikely case that populations in all patches happen to go extinct simultaneously, the species can survive by ping-ponging back and forth between patches. In contrast, for poor dispersers like yellowhead and robin, new colonists arrive rarely, and the light of the species winks out in one patch after another until all are gone.

### Bird Distributions in Mainland Forest Patches

The forest fragmentation and resulting local extinctions of bird populations that befell Banks Peninsula have been mirrored to varying degrees elsewhere in New Zealand. It is convenient for biogeographers, but sad for conservationists, that forest bird distributions on the New Zealand mainland now lend themselves to island biogeographic analyses. This approach has been pioneered by Dawson and Hackwell (1978; Hackwell and Dawson, 1980; Hackwell, 1982), some of whose conclusions may be briefly summarized.

Bird distributions in 177 Northland forest patches of varying sizes showed that species differ enormously in their incidences as a function of

area and isolation.  $A_{0.5}$  values are roughly in the following ranges:

- < 0.1 km<sup>2</sup>: fantail, grey warbler, silvereye
- 0.1 - 1 km<sup>2</sup>: pigeon, shining cuckoo, tui
- 1 - 10 km<sup>2</sup>: brown kiwi
- 10 - 100 km<sup>2</sup>: kaka, tomtit
- > 100 km<sup>2</sup>: red- and yellow-crowned parakeets, long-tailed cuckoo, kokako

In the same study a comparison of patches isolated to varying degrees from other forest patches showed that incidence of brown kiwi, parakeets, tomtit, tui, and kokako decreases with increasing isolation, while incidence of pigeon and fantail does not decrease over the range of isolations studied. Evidently, the former five species disperse less well overland than do the latter two.

Examination of 21 forest blocks of 20 - 1700 km<sup>2</sup> on North, South, and Stewart Islands revealed nine species present in all or most blocks, including the smallest: pigeon, shining cuckoo, rifleman, grey warbler, fantail, tomtit, bellbird, tui, and silvereye. The morepork is present in almost all blocks of area 70 km<sup>2</sup> or greater. Nine further species occur in few blocks, mainly large ones: kiwi sp., weka, kaka, red- and yellow-crowned parakeets, long-tailed cuckoo, robin, whitehead/yellowhead, and kokako.

Comparison of these incidences on mainland patches with those on land-bridge islands yields reasonable agreement for most species. The fantail, grey warbler, and silvereye, followed by pigeon, tui, shining cuckoo, and bellbird, recur in these various studies as champions at occupying small pieces of forest. All share the attributes of medium or high abundance, plus good ability to disperse both overland and overwater. Weka, kaka, long-tailed cuckoo, robin, whitehead/yellowhead, and kokako recur as species needing large pieces of forest. Some of these species require large areas because they are of low abundance, though good dispersers (kaka, long-tailed cuckoo); others, because they are poor dispersers, although of medium or high abundance (weka, robin, whitehead/yellowhead); and the kokako requires large areas for both reasons.

Two quantitative discrepancies between the island and mainland studies may be tentatively noted. Brown kiwi occupies mainland forest patches of 1 - 10 km<sup>2</sup> or even smaller but survived on no land-bridge island smaller than

Stewart (1735 km<sup>2</sup>). Naturally, kiwis can walk overland but not overwater. Perhaps kiwis are unlikely to persist in isolation for a long time on an isolated patch or island, but can maintain themselves in a system of isolated patches if dispersing individuals can occasionally walk from patch to patch. The other possible discrepancy is in the opposite direction. Red- and yellow-crowned parakeets on the mainland virtually require patches greater than 100 km<sup>2</sup> but occupy numerous islands smaller than 10 km<sup>2</sup>. My guess is that the island populations of parakeets are specialized for dispersal and genetically distinct from the mainland populations.

### Island Biogeography and Conservation Strategy

Many problems of bird conservation in New Zealand belong to either of two categories. On the one hand, some species such as taka he and kakapo are threatened and declining throughout their mainland ranges, principally as a result of predation, competition, or habitat damage by introduced mammals. On the other hand, many species of native forest birds are virtually tied to that habitat and are threatened mainly by its continuing destruction. These species include yellowhead, whitehead, kokako, robin, red- and yellow-crowned parakeets, kaka, kea, weka, brown kiwi, great spotted kiwi, and brown creeper.

The risks that these species face throughout New Zealand are exemplified by their fates on Banks Peninsula, where only one of them (brown creeper) survives, and on the land-bridge islands. They are threatened not just by the reduction in total area of their habitat, but also by the fragmentation of the remaining area into small pieces. The data assembled in this paper show that certain forest species tend to disappear again and again, whenever forests are fragmented. The list of these fragmentation-sensitive species proves to be identical to the list of native forest species threatened by forest destruction. Conversely, when New Zealand forests are fragmented, one ends up again and again with the same species: the fantail, grey warbler, silvereye, and others. These species occur in forest scraps and gardens throughout New Zealand. They are the most abundant native New Zealand birds and do not require protective measures.

The message of these studies is clear: the fate of New Zealand's forest bird species hangs on

preserving large tracts of native forest. From the perspective of forest bird conservation, small forest patches are of much lower value. This conclusion has been recognized for New Zealand by Fleming (1975), Dawson and Hackwell (1978), Hackwell and Dawson (1980), and East and Williams (1984). The same conclusion has been reached for forests elsewhere in the world by other conservation biologists (Wilson and Willis, 1975; Terborgh, 1974, 1975; Diamond, 1975a, 1976a; Wilcox, 1980; Willis, 1980; Whitcomb *et al.* 1981).

Simberloff and Abele (1976) attacked this preference for large reserves on the basis of the following specious reasoning. They calculated from species/area relationships that one large reserve might contain more or fewer species than the equivalent area in small reserves, and that therefore island biogeography was neutral on the question of optimal reserve size. I am not aware of anyone having proposed total species number as the argument favoring large over multiple small reserves, until Simberloff and Abele set up the argument as a straw man. Several groups of authors (Terborgh, 1976, Whitcomb *et al.*, 1976, Diamond, 1976b) immediately responded that the relevant criterion is number of species that a conservation program saves and that would otherwise be endangered. A New Zealand forest reserve that held 15 species like fantail, silvereye, and grey warbler, while losing two species like kokako and yellowhead, would rate as a disaster. Nevertheless, Simberloff and Abele (1982) continued in a subsequent paper to ignore this fact and to pretend that the relevant criterion is total species number.

More recently, Simberloff and Abele (1982) produced another theoretical argument purporting to show that one large reserve has no advantage over several small ones. They claim that populations larger than 20 individuals are virtually immune from extinction, hence a reserve would be adequately large provided only that it could hold 20 individuals! The fallacy underlying this patently absurd claim is that the calculations of extinction probabilities by Simberloff and Abele invoke a population model (Richter-Dyn and Goel, 1972) which considers only demographic fluctuations, the main cause of extinction in very small populations, and which ignores environmental fluctuations, the main cause of extinction in large populations (Leigh, 1981).

A final theme in this debate is the argument

repeatedly advanced by Simberloff and Abele that conservation strategies should not be based on biogeographic principles but on detailed autecological studies of single species. No one questions the value of such studies wherever money and time are available. However, in most real situations this argument reminds me of Andrew Marvell's poem "Had we but world enough, and time". With these words as a start, the poet tells his coy mistress that he would woo her by spending 100 years praising each of her eyes, 200 years adoring each breast. . . but he and she would both be dead by then, so she should decide quickly. Conservation biologists face the same problem. In New Zealand, as elsewhere in the world, decisions about logging are being made now, and the forests would be felled while we awaited the outcome of detailed autecological studies. Like Marvell's mistress, we need to decide quickly, based on what we know now.

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