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COLONIZATION OF THE KRAKATAU ISLANDS BY LAND BIRDS, AND THE APPROACH TO AN EQUILIBRIUM NUMBER OF SPECIES

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CONTENTS

The colonization of the Krakataus by resident land birds is re-examined in view of two additional good data points, 1951 and 1984–86, which were not available to MacArthur & Wilson (1967) in their seminal work on island biogeography. The bird data for all years were carefully assessed with respect to the explicit criteria needed for the calculation of rates of extinction, immigration and turnover; these parameters are defined and calculated.

Calculated from data from the two most recent surveys, the equilibrium number of species ($\hat{S}$) for Rakata, the largest island, is from 48 to 56 and for the archipelago as a whole from 44 to 58; the ranges reflect alternative assessments of the records. By fitting a colonization equation to data from all surveys, $\hat{S}$ for the archipelago is estimated as 36 species, and by a procedure attempting to account for cryptoturnover, 38 species. These estimates compare with 30 (MacArthur & Wilson 1967) and 40–45 (Mayr 1965). Thirty-seven species were present during 1984–86.

The establishment of the secondary forest and closure of the canopy had the greatest effect on colonization parameters of resident land birds since 1883. Immigration and turnover peaked in the period 1908–21 and fell sharply over the next decade, when, in contrast, extinctions reached a peak.

The species that have colonized the Krakataus are mostly wide-ranging species that are found in both Java and Sumatra and have wide ecological tolerances. The earlier colonists were open country, generalist species, but since forest formation there was an increase in the proportion that are true forest species and more specialist feeders; more recent colonists have been aerial predators and insect feeders. Analysis of the colonization data suggests that the first resident land birds colonized the Krakataus one or two decades after the 1883 eruption.

The newly emergent island, Anak Krakatau, has provided early seral habitats for species that have been lost from the other islands of the archipelago because of ecological succession and consequently the island provides an ecological refuge, postponing the extinction of birds that depend on these open habitats. Anak Krakatau's emergence and continued existence will reduce species turnover and delay the achievement of equilibrium on the archipelago.

1. Introduction

Birds, like butterflies (see, for example, New *et al.* 1988), have several advantages as a group of organisms on which to carry out studies on colonization and turnover. They are mobile, generally conspicuous, and individuals and species usually exist in substantial numbers. They have thus attracted the attention of biologists since the days of the early explorer-naturalists, and are now sufficiently well-known taxonomically to be identified more easily and with a higher degree of reliability than is the case with most other animal groups, even in tropical areas. Survey methods are formalized and to a large degree repeatable, and in many cases identifications may be made on either visual or auditory evidence. Specimens may be fairly readily collected, and field aids to identification are usually available; hence, birds have been extensively studied in many areas and the geographical ranges of many species can be defined with some precision. Moreover, evidence of breeding is shown in a number of ways such as nesting, courtship and feeding of young. It is therefore not surprising that the majority of studies on problems of island biogeography have concerned birds.

In studies of recolonization and approach to equilibrium numbers of species on the Krakataus since the sterilizing cataclysmic eruption of 1883 (see Thornton & Rosengren 1988), birds have a pre-eminent importance for several reasons.

Before the classical experimental studies of Simberloff & Wilson (1970) had been made, MacArthur & Wilson (1963, 1967) used the birds of the Krakataus as a key test of their equilibrium model of colonization and turnover on islands, and their conclusions on the approach to equilibrium of the Krakatau bird fauna have been widely quoted in biogeography texts (see, for example, MacArthur & Connell 1966; Gorman 1979; Cox & Moore 1980; Williamson 1981; Ehrlich & Ehrlich 1982; Brown & Gibson 1983). Thus continuing studies of Krakatau birds are of interest to biogeographers in general, as well as to bird specialists.

Birds are unique among the animal groups of the archipelago in having been the subject of a specialist survey in 1951 (Hoogerwerf 1953*a*), some two decades after the work of Dammerman's group on the islands ended in 1933 (Dammerman 1948). The ornithologist Hoogerwerf spent nine days on the island in 1951, mainly on Rakata (10 h on Sertung, 20 min on Panjang) and his survey has provided a crucial data point, about mid-way between 1933 and the 1980s, that is not available for other animal groups.

In addition, the bird fauna of an exemplar source area, the Ujung Kulon peninsula of west Java (figure 1), a wilderness area of some 300 km^2 that has been a wildlife sanctuary since 1921 and together with the Krakataus is now a National Park, has also been reliably surveyed by the same ornithologist as a result of regular visits totalling approximately 450 days from 1937 to 1958 (Hoogerwerf 1953*b*, 1970*a*).

Finally, birds have an importance because of their possible role in the colonization of other organisms, particularly plants. Along with frugivorous bats, fruit-eating birds may have a substantial effect on plant colonization and vegetational succession (Snow 1981; Finegan 1984), which in turn may have far-reaching implications for the development of the succession of many groups of organisms, including birds themselves.

Thus from a biogeographical point of view birds are probably the most important group of animals on the archipelago. Whereas the Japanese expedition of 1982 surveyed several animal groups (Yukawa *et al.* 1984), it did not include an ornithologist. Bush & Newsome (1986) provided a list of incidental observations of birds on the archipelago by the Hull University botanical expeditions of 1979 and 1983. Ibkar-Kramadibrata *et al.* (1986) also listed the birds noted by the 1982 biological expedition from the Institute of Technology, Bandung, which spent seven days on Panjang and Anak Krakatau. However, on neither the Hull nor the Bandung expeditions was a bird survey conducted. One of the main objectives of our 1984–1986 expeditions was to fill this important gap by making as thorough a survey as possible of the Krakatau birds so that comparisons with earlier and future surveys could be made.

This paper is one in a series on the birds of the Krakatau islands. The first paper (Zann *et al.* 1990*a*) lists the species found for the period 1984–86 and describes their distribution by island and habitat. In this paper we re-examine MacArthur & Wilson's conclusions on the recolonization of the Krakataus by birds in relation to species turnover and the approach to equilibrium in view of two additional good data points: Hoogerwerf's 1951 data and the new data for 1984–86. Another paper (Zann *et al.* 1990*b*) describes in detail the abundance, distribution and ecological aspects of birds on the newly emergent island, Anak Krakatau.

2. Methods and coverage

The 1984 survey (Zann *et al.* 1990*a*) was made in September by four ornithologists, three of whom had previously worked in Indonesia and Malaysia. The 1985 survey was carried out in August by R.A.Z. who had also taken part in the 1984 expedition. During the expedition in September 1986, two ornithologists concentrated their attention on Anak Krakatau.

Details of survey methods and coverage in 1984 and 1985 are provided in Zann *et al.* (1990*a*), and are summarized in table 1.

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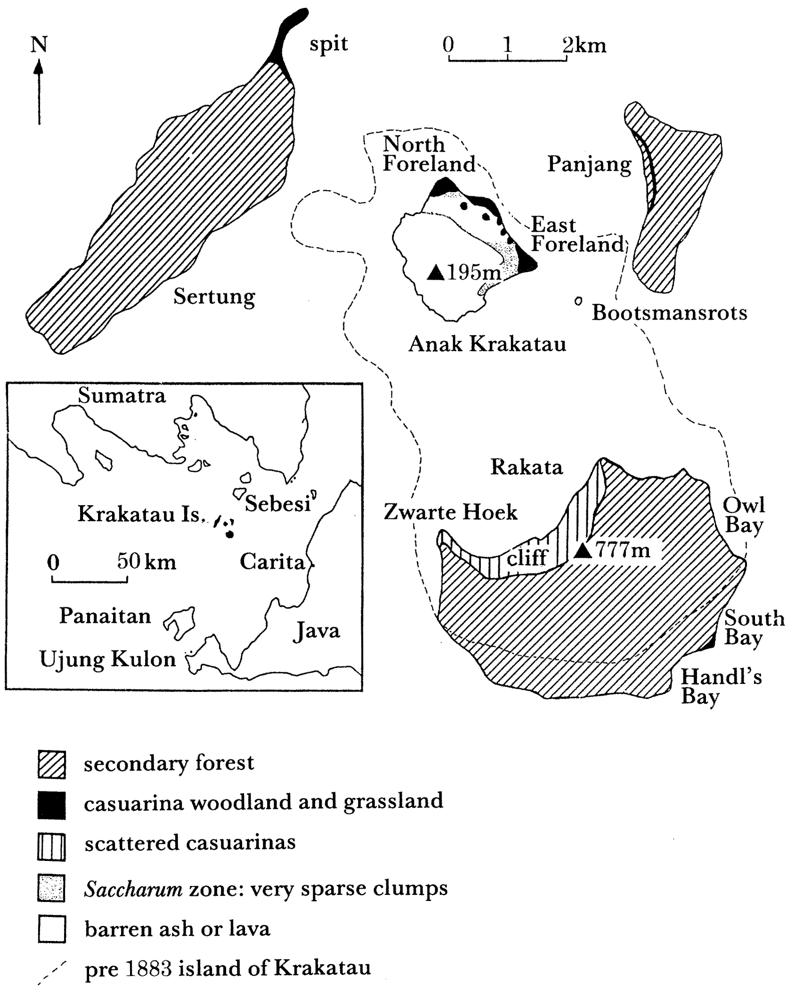

FIGURE 1. Sunda Strait and the Krakatau Islands, showing places mentioned in text and vegetation on the Krakataus.

3. Evaluation of extinction, immigration and turnover

In an interesting discussion paper, Lynch & Johnson (1974) suggested that a set of explicit criteria should be applied to studies of turnover that depend on repeated surveys. Bearing in mind that any turnover found in the Krakatau fauna until now will probably have been successional, rather than equilibrium turnover, we discuss these criteria in the context of Krakatau surveys.

(*a*) *Extinction*

Lynch & Johnson suggested that the absence in one survey of a species that was present in the preceding one can only be counted as a valid extinction if all the following conditions are met:

1. The resident status of the species at the time of the earlier survey is reasonably certain. In the case of the Krakatau fauna, we have omitted marine birds, shorebirds and known migrants from considerations of turnover, and have counted as resident only those species (henceforth designated resident land birds) for which some evidence of breeding on the islands

Table 1. Duration and intensity of bird survey methods at study sites from 1984 to 1986

(Spotlighting in brackets, mist-netting measured as square metres of net multiplied by rain-free hours set, visual survey in man-hours. T, total for all years. The following sound recordings were also made; 1984: 1 h Rakata, 2 h Anak Krakatau; 1985: 1 h Sertung, 2 h Panjang and 3 h Anak Krakatau. See Zann *et al.* (1990*a*) for further details.)

	visual survey				mist-netting			
island site	84	85	86	T	84	85	86	T
Rakata Zwarte Hoek	48 (6)	—	—	48 (6)	3446	—	—	34
West Ridge to 250 m	42 (4)	—	—	42 (4)	1011	—	—	10
West Ridge 250–777 m	25	—	—	25	—	—	—	—
Owl Bay	—	12	—	12	—	—	—	—
South Bay	34 (4)	3	—	37 (4)	1456	144	—	16
Handl's Bay	—	0.4	—	0.4	—	—	—	—
eastern ascent	—	4	—	4	—	—	—	—
summit	—	10	—	10	—	—	—	—
southern descent	—	3	—	3	—	—	—	—
total	149 (14)	32.4	—	181.4 (14)	5913	144	—	60
Sertung Spit	38	6	—	44	260	699	—	9
northern forest	—	7	—	7	—	558	—	5
total	38	13	—	51	260	1257	—	15
Panjang north	17	2	—	19	284	—	—	2
northwest	—	15 (2)	—	15 (2)	—	504	—	5
central west	—	11 (2)	—	11 (2)	—	—	—	—
total	17	28 (4)	—	45 (4)	284	504	—	7
Anak Krakatau	47 (5)	32 (1)	61 (14)	79 (6)	2272	390	10879	135
Bootsmansrots	0.3	—	—	0.3	—	—	—	—
Total Krakataus	251.3 (19)	105.4 (5)	61 (14)	356.7 (24)	8729	2295	10879	302

was found or has been reported, and others known to be resident in west Java and southern Sumatra (van Oort 1910; Bartels 1919; Chasen 1937; de Jong 1938; Dammerman 1948; Hoogerwerf 1947, 1949*a*, *b*, 1953*a*, *b*, 1970*a*, *b*; Blower & van der Zon 1977; Anon 1980, 1981, 1982; Mitchell 1981; de Wulf *et al.* 1981; MacKinnon 1988; van Marle & Voous 1988).

2. There must be evidence of the absence of the species at the time of the later survey. Proof of absence is difficult to provide; absence of evidence is not evidence of absence. Charles Kingsley (1889) wrote: 'And no one has a right to say that no water-babies exist, till they have seen no water-babies existing; which is a different thing, mind, from not seeing water babies'. In a good survey, methods and coverage are specified and judgements made about the reality of apparent absences can be assessed by other workers. We have attempted to provide such details, and where necessary make such judgements, with reasons.

3. Human influence must not have played a significant role in the species' demise. The extent of human influence on the Krakataus is treated in the introductory paper of this series (Thornton & Rosengren 1988). It has been very slight, and unlikely to have affected the possibility of extinction of any bird species.

4. Natural successional changes in habitat must not have been an important influence. Lynch and Johnson (1974) were treating equilibrium turnover. On the Krakataus successional turnover has been predominant; the problem is to recognize equilibrium turnover when it occurs, and to distinguish it from successional turnover. This criterion clearly does not apply to the Krakataus work.

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(*b*) *Immigration*

Lynch and Johnson's criteria for valid immigration include:

1. There must be a reasonable certainty that the species was absent at the time of the earlier survey. The above comments under extinction (2) apply, and in applying this criterion we must rely on information provided by previous workers. We make judgements in some cases, and give reasons for these.

2. There must be specific evidence of a breeding population during the later survey. Lynch & Johnson suggest that this criterion is met if the presence of at least one breeding pair can be established, and that evidence of breeding would include nesting records, recently fledged young attended by parents, preferably with voucher specimens, singing males (less reliable) and gonad condition. As stated below we took minimal voucher specimens. We must rely on previous workers for such evidence in the case of earlier surveys, and Zann *et al.* (1990*a*) cite such evidence from our surveys. We have not followed this criterion as strictly as Lynch & Johnson suggest, and discuss this further below.

(*c*) *Turnover*

Estimates of turnover rates (rate of change in species complement) based on surveys made many years apart will miss 'in-and-out' species (Jones & Diamond 1976), which will then be undocumented (cryptoturnover). Such estimates will thus be minimal ones (Lynch & Johnson 1974), revealing only the 'tip of the iceberg'. Jones & Diamond also point out that the effect of lumping several years into one survey (as we do, following previous authors, by identifying two survey 'periods' within the years of Dammerman's surveys) for comparison with a single survey (for example, that of Hoogerwerf), is to overestimate extinctions, but to underestimate immigrations and so these tend to cancel each another.

We can do nothing to change history, and must accept the data from surveys that have been made, making the best possible use of them under the circumstances. We combine our 1984, 1985 and 1986 surveys, believing this appropriate in the context of previous surveys, but note and discuss possible differences between the years. Jones & Diamond (1976) and Diamond & May (1977) advocate annual surveys to obtain even approximately accurate estimates of turnover rates. We agree that this course would be ideal, but unfortunately resources are not. We also believe that such frequent surveys may be more important in the case of studies examining the possibility of equilibrium turnover than those investigating the much less controversial successional turnover, which is predominant in this study. Moreover, the effect of annual scientific expeditions on the biota of an archipelago as small as the Krakataus must be considered.

In approaching the question of successional turnover and achievement of equilibrium in the avifauna, we confine ourselves to resident land birds, as defined above. An extreme conservative approach would also exclude all species for which there is no evidence of breeding (cf. Lynch & Johnson 1974). This would exclude from consideration 24 out of the 45 resident land bird species ever known from the archipelago (table 2), many of which have been on the islands in every survey that has been recorded, and in none of the 21 for which there is evidence of breeding on the islands is the evidence available for all surveys. Of the 36 resident land bird species present in the 1980s, for only 20 is there evidence of breeding on the islands, and for only 16 at the time of our surveys. We believe that an approach to the data of such conservatism would negate the efforts of many previous workers and be almost completely unproductive.

We therefore provide two analyses below, one counting all resident land bird species recorded, and the other based on conservative judgements of our own and previous surveys, as to resident status. By providing as much field data as possible (Zann *et al.* 1990*a*), we allow other workers to make their own assessments of our judgements concerning our surveys.

4. Definition and calculation of turnover rates

(*a*) *Rate coefficients of immigration, extinction and colonization*

Rate coefficients of immigration, extinction and colonization take account of the size of the faunas concerned and thus, to a degree, allow comparisons between animal groups on the same island, or between the same group on different islands. It is therefore necessary that the definitions and methods used for calculation of these rate coefficients are explicitly stated, and this is particularly important when comparisons are made with the results of other workers.

(i) *Rate coefficient of immigration* (*or acquisition*)

To calculate a rate coefficient of immigration (λ_s), Diamond (1971), in comparing equilibrium turnover rates of tropical and temperate islands, used the formula

$$\lambda_{sp} = I/\{P-[(S_1+S_2)/2]\} \qquad (1)$$

where I is the number of immigrants per year, P the number of species in the mainland pool, and S_1 and S_2 the number of species present in successive censuses. Abbot & Grant (1976) used this formula, modified to allow for two species pools, in their analysis of the land bird faunas of islands (for which they found evidence of non-equilibrium) off Australia and New Zealand. The number of mainland species that are already on the island, which therefore cannot add to its species number and so must be excluded from the available pool, is calculated as the average number of the two censuses. Thus the number of immigrant species per year is expressed as a proportion of the average number of species in the mainland pool that is available to add to the species number on the island during the intersurvey period. We will use the term 'pool immigration rate coefficient' from now on for this proportional rate of immigration from a known potential species pool.

There are practical problems with this coefficient. First, although the size of the available pool of potential immigrants may often be an important factor to be taken into account, as when rates for islands with different immigration pools are to be compared (see, for example, Diamond 1971), sometimes the pool itself cannot be identified or its limits defined, and even when the pool is obvious and definable the size of its fauna may not be known. In the present case, although the bird fauna of Ujung Kulon Wildlife Reserve on the western tip of Java is fairly well known and it is most probably the most important source area for the Krakataus, it cannot be assumed to be the only one. Other parts of west Java and of southern Sumatra may have contributed to varying extents; however, as seen from table 8 (§6*a*), the contribution from southern Sumatran species that do not also occur at Ujung Kulon has been minimal.

The second problem is one of mathematical convenience. λ_{sp} cannot be simply related to rate coefficients of extinction, colonization and turnover, because of the inclusion of available pool numbers in this equation alone (see below).

We use this rate coefficient below, however (§ 6*c* and § 7*b*), in estimating expected equilibrium number of species.

Whittaker & Flenley (1982), in their discussion of plant immigration rates on the Krakataus, evidently used the equation

$$\lambda_{s_2} = I/S_2 \tag{2}$$

which expresses annual number of additional species as a proportion of the species number on the island at the end of the period during which immigration has occurred. λ_{s_2}, and $\lambda_{\bar{s}}$ (below), differ conceptually from λ_{sp} (equation 1) in that they relate an observed increase in species number to the number on the island, rather than to that in the available pool, and this distinction may perhaps usefully be underlined by a different designation 'island acquisition rate coefficient', or, more simply, 'acquisition rate coefficient'. Richards (1986) uses modifications of this basic formula.

We believe that if the number of immigrant species during an intersurvey period is to be related to numbers on the island rather than to numbers of potential immigrants, in non-equilibrium situations it should be related to average numbers present on the island during the period, thus recognizing that numbers on the island may change (partly through the immigration itself) during the period. We have therefore used the formula

$$\lambda_{\bar{s}} = I/[(S_1+S_2)/2] \tag{3}$$

where $\lambda_{\bar{s}}$ is acquisition rate coefficient.

(ii) *Extinction rate coefficient*

To calculate the extinction rate coefficient ($\mu_{\bar{s}}$), Diamond (1971) and Abbot & Grant (1976), used the equation:

$$\mu_{\bar{s}} = E/[(S_1+S_2)/2], \tag{4}$$

where E is the number of extinctions per year. This equation, like equations (1) and (3), takes into account the changing number of species during the intersurvey interval.

From the statements of Whittaker & Flenley (1982), it is apparent that they used the equation suggested by MacArthur & Wilson (1967, table 5 therein) instead, and Richards (1986) also uses this basic equation:

$$\mu_{s_1} = E/S_1. \tag{5}$$

This rate coefficient expresses extinction rate as a proportion of the precise number of species available to become extinct (that is, present at the beginning of the interval), but does not take into account the fact that the extinctions may have occurred at any time during the interval between surveys, when species number may not have been S_1. We prefer to account for this by using equation (4).

Objections to the use of the average number of species during the intersurvey interval in equations (3) and (4) may be raised on the grounds that, in contrast to equilibrium situations, in seral situations when species numbers may rise massively between surveys, $\mu_{\bar{s}}$ becomes mainly a function of increase in species numbers, that is, the acquisition rate coefficient. We agree, but point out that the two are probably also interrelated in nature, so that it is in seral situations that the use of the closest possible estimate of the continuum of changing species number during the intersurvey period is particularly appropriate.

(iii) *Colonization rate coefficient*

If equations (3) and (4) are used ($\lambda_{\bar{s}}$ and $\mu_{\bar{s}}$, respectively) then colonization rate coefficient (γ), calculated as

$$\gamma = (I-E)/[(S_1+S_2)/2] \tag{6}$$

becomes

$$\gamma = \lambda_{\bar{s}} - \mu_{\bar{s}}. \tag{7}$$

Colonization rate coefficient is thus the difference between the rate coefficients of island acquisition and extinction.

Whittaker & Flenley (1982), although calculating λ_s and μ_s by methods different from those we have chosen to use, designated this as percentage rate of increase of observed species number, which in their case $= \lambda_{s_2} - \mu_{s_1}$.

(b) *Turnover and turnover rates*

(i) *Turnover*

Turnover has been defined as the number of species replaced (Whittaker & Flenley 1982), a definition that has both simplicity and intuitive appeal. By this definition turnover will be the lesser of immigration and extinction. In several equilibrium studies (see, for example, Diamond 1969; Brown & Kodric-Brown 1972; Hunt & Hunt 1974) turnover has been regarded as the average of the number of immigrants and extinctions, a definition that involves the full range of changes in species complement. We are using the latter definition.

The difference between the time curves of actual and cumulative species numbers is sometimes also treated as turnover (see, for example, Flenley & Richards 1982). Where there are re-immigrations, however, as shown in figure 2, this difference equals the number of extinctions (not the number of replacements), at the time of a particular survey, of the species present in all previous surveys. It does not necessarily represent turnover, either in the sense of extinctions or replacements (which in figure 2 are the same), for any intersurvey period after the first two, in which periods there can be no recorded reimmigrations.

(ii) *Turnover rate*

In considering the approach of the Krakatau flora to equilibrium, Whittaker & Flenley (1982) defined turnover rate (T), following from their definition of turnover, as the number of species replaced per year, which is of course the smaller of their immigration rate and extinction rate. Turnover rate has also been calculated as the average number of immigrants and extinctions per unit time in studies of the avifaunas (Diamond 1969; Hunt & Hunt 1974) and mammal faunas (Crowell 1986) of islands at equilibrium and of non-breeding arthropods on isolated thistle plants apparently at equilibrium (Brown & Kodric-Brown 1972). We also calculate turnover rate in this way.

(iii) *Turnover rate coefficient*

The concept of relative turnover rate, to take into account faunal size, was proposed by Diamond (1969).

From their statements, Whittaker & Flenley (1982), dealing with successional turnover,

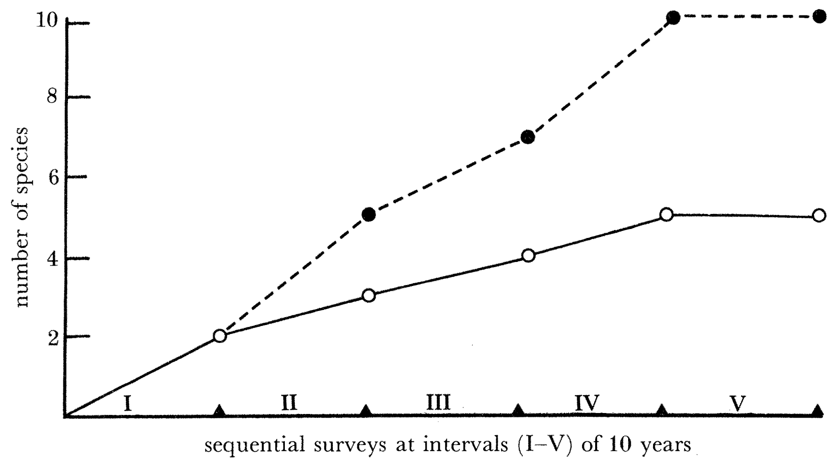

FIGURE 2. Hypothetical colonization curves derived from different data bases (A) and (B). The difference between cumulative and actual curves equals the cumulative number of species that have become extinct, but not necessarily replaced, at the time of a given survey compared to all prior surveys. It does not necessarily represent turnover in the interval between successive surveys. Open circles, actual curve; closed circles, cumulative curve.

survey	1	2	3	4	5
data base (A)					no turnover
species present	(a) (b)	(c) (d) (e)	(f) (g) (d) (e)	(a) (c) (h) (i) (j)	(a) (c) (h) (i) (j)
number of species extinct (replaced) cf. preceding survey		2	1	4	0
number of species replaced cf. all prior surveys		2	2	3	0
number of extinctions cf. all prior surveys		2	3	5	5
data base (B)					total turnover
species present	a b	(c) (d) (e)	(a) (c) (f) (g)	(a) (d) (h) (i) (j)	(b) (c) (e) (f) (g)
number of species extinct (replaced) cf. preceding survey		2	2	3	5
number of species replaced cf. all prior surveys		2	2	3	0
number of extinctions cf. all prior surveys		2	3	5	5

evidently calculated percentage turnover rate (% T) by a method selected also by Gorman (1979) and followed by Richards (1986).

$$\%\ T = [\text{number of species replaced per year } (= \text{the smaller of } E \text{ and } I)/S_2] \times 100. \quad (8)$$

Correcting for the changing numbers during the interval between surveys this may be modified to

$$\%\ T = \{[E \text{ or } I \text{ (whichever is the smaller)}/(S_1+S_2)]/2\} \times 100, \quad (9)$$

% T, or τ, turnover rate coefficient, would thus be the smaller of $\lambda_{\bar{s}}$ and $\mu_{\bar{s}}$.

The following equation was used by Diamond (1969), Hunt & Hunt (1974), Brown &

Kodric-Brown (1972), Jones & Diamond (1976) and Schoener (1983) in a review of turnover in over a score of equilibrium situations, and by Crowell (1986), comparing relict and equilibrium models for insular mammal faunas:

$$\%\, T = (E+I)/(S_1+S_2) \times 100. \qquad (10)$$

This may be rewritten as:

$$\%\, T = [(E+I)/2]/[(S_1+S_2)/2] \times 100. \qquad (11)$$

Turnover rate coefficient calculated in this way is thus the average number of incoming and outgoing species per year as a proportion of the average number of species on the island during the inter-census interval. Whittaker & Flenley's (1982) equation (9) (and Richards' (1986) equation 5) will give the same result only at equilibrium, when $S_1 = S_2$.

We believe that equation (11) is preferable in situations of successional turnover. By using equations (3) and (4) this may be rewritten as

$$\tau = (\lambda_{\bar{s}} + \mu_{\bar{s}})/2 \qquad (12)$$

or, turnover rate coefficient is the average of the coefficients of acquisition and extinction.

5. Faunal changes on the archipelago, 1883–1986

(a) *Consideration of 'gains' and 'losses'*, 1883–1986

Table 2 lists all species of resident land birds recorded on the Krakataus from Jacobson's survey of 1908 (Jacobson 1909) up to 1986. Evidence of breeding, shown by an asterisk, is detailed in another paper of this series (Zann *et al.* 1990*a*). Non-resident species excluded from the list, comprising marine birds, shorebirds, stragglers, and those land birds Hoogerwerf (1970*b*) considered migrants in the Sumatra–Java region of Indonesia, are listed in table 3. Based on table 2, acquisition, extinction, turnover and pool immigration rate coefficients over the period 1883 to 1986 are as shown in tables 5 and 6.

(i) *First survey*, 1908 (*Jacobson*)

Jacobson visited the islands (chiefly Rakata) for three days in late May 1908, the end of the migratory period, and of the 16 species recorded, one, *Actitis hypoleucos*, was a migrant, and two were terns (table 3). Jacobson had no specialist ornithologist, and there is evidence of breeding for only two species, the nightjar, *Caprimulgus affinis*, and the extremely abundant black-naped oriole, *Oriolus chinensis*, although Dammerman (1948) regards 11 out of the 13 non-migrant non-marine species as having been 'permanent dwellers'. The two species that Dammerman thought may not have been 'permanent settlers' are the small blue kingfisher, *Alcedo caerulescens* and gold-vented bulbul, *Pycnonotus aurigaster*. Both are clearly recognizable. They were not found in subsequent surveys but we accept their residence in 1908.

It is possible (see below) that three species found in 1919–1922 may have been missed by Jacobson. The minimum number in 1908 can thus be taken as 13 species, with a high of perhaps 16, although this short non-specialist survey must be regarded as a minimum estimate. For the calculation of rates based on assessments below (table 6), we accept 16, and on the records (table 5), 13.

TABLE 2. RESIDENT LAND BIRDS OF THE KRAKATAUS, 1883–1986

	1908	1919–21	1932–34	1951–52	1984–86
1. *Alcedo caerulescens*	R	—	—	—	—
2. *Pycnonotus aurigaster*	R	—	—	—	—
3. *Lanius schach**	R	R*S*	—	—	—
4. *Corvus macrorhynchos*	RP	RS	RSP	S	R[b]A
5. *Centropus bengalensis**	R	R*S	R*S*	R	SP[c]A
6. *Treron vernans**	R	RS	RSP	S	RSPA*
7. *Caprimulgus affinis**	R*	R*S*	RS*	A	RSPA
8. *Chalcophaps indica**	R	R*S*	R*S	R	RSP
9. *Collocalia fuciphaga*	RP	RS	RS	R	RSPA
10. *Halcyon chloris**	R	R*S*	RSP	R*	R*S*P*A*
11. *Pycnonotus goiavier**	R	RS	RS*P	RA	R*S*P*A*
12. *Oriolus chinensis**	R*SP	R*S	RSP	R	RSPA*
13. *Artamus leucorhynchus**	RP	RS	RS	R	RSPA*
14. *Centropus sinensis*	+	S	—	—	—
15. *Accipiter trivirgatus*	+	R	S	—	—
16. *Geopelia striata*	+	R	+	S	—
17. *Eudynamys scolopacea*	—	RS	RSP	R	—
18. *Ducula bicolor*	—	RS	RS	—	RSP
19. *Hirundo tahitica*	—	RS	RS	+	RSA
20. *Amaurornis phoenicurus**	—	R*S*	R*S*P	R*S	A*
21. *Haliastur indus**	—	R*S*	R*	S	R
22. *Haliaeetus leucogaster**	—	R*S*	R*S*P	R*SA	R*SP*A
23. *Picoides moluccensis*	—	R	RS	R	SP
24. *Lalage nigra*	—	RS	RS	R	RP
25. *Copsychus saularis**	—	RS	RS	R	RSP*A*
26. *Pachycephala cinerea**	—	RS	RS	R	R*S*PA*
27. *Aplonis panayensis**	—	RS*	RSP	R	R*SPA
28. *Anthreptes malacensis*	—	RS	RS	R	RSPA
29. *Nectarinia jugularis**	—	RS*	RSP	R	RSP*A*
30. *Dicaeum trigonostigma*	—	RS	RS	R	R
31. *Macropygia phasianella**	—	—	S	R*	RS*PA
32. *Collocalia esculenta**	—	—	R	R	RP*
33. *Gerygone sulphurea**	—	—	RSP	R	RSPA*
34. *Cyornis rufigastra**	—	—	RS*P	R	R*S*PA*
35. *Spilornis cheela*	—	—	—	R	—
36. *Rhaphidura leucopygialis*	—	—	—	R	+
37. *Ptilinopus melanospila*	—	—	—	R	RP
38. *Aethopyga mystacalis*	—	—	—	RS	RP
39. *Pycnonotus plumosus*	—	—	—	RS	RS
40. *Falco severus**	—	—	—	S	R[a]A*
41. *Ictinaëtus malayensis*	—	—	—	—	RSP
42. *Ducula aena*	—	—	—	—	RS[b]P
43. *Tyto alba*	—	—	—	—	RSA
44. *Apus affinis*	—	—	—	—	RSPA
45. *Zoothera interpres*	—	—	—	—	RA

(*, Evidence of breeding; +, presence counted on assessment.)
[a] seen 1982 by A. Compost, not seen by us.
[b] recorded 1983 by Bush & Newsome (1986), not seen by us.
[c] recorded 1982 by Ibkar-Kramadibrata *et al.* (1986), not seen by us.
In this and subsequent tables: R, Rakata; S, Sertung; P, Panjang; A, Anak Krakatau; B, Bootsmansrots.

(ii) *Second survey*, 1919–1922 (*Dammerman*)

In April 1919, Bartels (1919) surveyed the bird fauna in five days, three on Rakata, two on Sertung (Docters van Leeuwen 1921), recording a total of 32 species, and Siebers spent four days on Rakata and two on Sertung in September 1920. Both were experienced ornithologists. Siebers' visit, and other observations by Dammerman's group from October 1919 to January

TABLE 3. MIGRANT (MI), MARINE (MA), SHOREBIRDS (SH) AND STRAGGLERS (ST) ON THE KRAKATAUS, 1883–1986

species	1908	1919–21	1930–34	1951–52	1984–86
1. *Actitis hypoleucos* (MI, SH)	S	RS	RS	RSA	RSPA
2. *Sterna dougalli* (MA)	SB	S	—	—	B
3. *Sterna sumatrana* (MA)	SB	S	R	R	P[a]B
4. *Fregata* sp. (MA)	R	R	—	—	—
5. *Oceanodroma leucorhoa* (MA)	—	S	—	—	—
6. *Apus pacificus* (MI)	—	S	—	—	—
7. *Lanius cristatus* (MI)	—	R	—	—	—
8. *Butorides striatus* (SH)	—	S	S	—	—
9. *Motacilla flava* (MI)	—	RS	S	—	—
10. *Numenius phaeopus* (MI, SH)	—	R	—	A	—
11. *Egretta sacra* (SH)	—	RSB	S	—	RSPA
12. *Charadrius leschenaultii* (SH, ST)	—	S	SA	—	RS
13. *Esacus magnirostris** (SH)	—	S	SA	RS*A	RSPA
14. *Chlidonias leucoptera* (MA)	—	RSB	—	—	x
15. *Sterna anaethetus* (MA)	—	S	S	—	R
16. *S. bergii* (MA)	—	SB	S	—	A[a]B
17. *Hirundo rustica* (MI)	—	RS	RS	RSA	RPA
18. *Charadrius dubius* (MI, SH)	—	—	S	—	—
19. *Tringa nebularia* (MI, SH)	—	—	S	—	—
20. *Alcedo atthis* (MI, SH)	—	—	S	—	—
21. *Acrocephalus arundinaceus* (MI, ST)	—	—	R	—	—
22. *Muscicapa latirostris* (MI)	—	—	S	—	—
23. *Ficedula narcissina* (MI)	—	—	R	—	—
24. *Pluvialis dominica* (MI, SH)	—	—	S	A	—
25. *Arenaria interpres* (MI, SH)	—	—	S	R	—
26. *Accipiter virgatus* (MI)	—	—	—	S	—
27. *Charadrius mongolus* (MI, SH)	—	—	—	A	—
28. *Calidris tenuirostris* (MI, SH)	—	—	—	A	—
29. *Merops superciliosus* (MI, ST)	—	—	—	S	—
30. *Motacilla cinerea* (MI)	—	—	—	RA	A
31. *Fregata ariel* (MA)	—	—	—	—	RSPA
32. *Fregata minor* (MA)	—	—	—	—	x
33. *Chlidonias hybrida* (MA)	—	—	—	—	x
34. *Sterna albifrons* (MA)	—	—	—	—	x
35. *S. fuscata* (MA)	—	—	—	—	x[a]
36. *S. hirundo* (MA)	—	—	—	—	x
37. *Corvus splendens* (ST)	—	—	—	—	A
38. *Gallus gallus* (ST)	—	—	—	—	A[b]
39. *Phylloscopus* sp. (MI, ST)	—	—	—	—	A
40. *Lanius tigrinus* (MI, ST)	—	—	—	—	A

(*, evidence of breeding; x, at sea near islands.)
[a] seen by Bush & Newsome (1986), but not by us.
[b] seen by Ibkar-Kramadibrata *et al.* (1986), not established.

1922, during which time 16 days were spent on Rakata and 12 on Sertung by non-ornithologists, brought the total to 45 species, of which 28 were resident land birds. There is evidence of breeding for 11 of the land birds during the period (Chasen 1937; Dammerman 1948).

Several species newly recorded in this period are unlikely to have been missed by Jacobson had they been present in 1908. These include the koel, *Eudynamys scolopacea* (with a loud characteristic call); pied imperial pigeon, *Ducula bicolor* (conspicuous, usually in flocks); Pacific swallow, *Hirundo tahitica* (easily recognized, observed frequently); white-breasted waterhen, *Amaurornis phoenicurus* (furtive, but with an unmistakable call); brahminy kite, *Haliastur indus*, and white-bellied sea eagle, *Haliaeetus leucogaster*, with Dammerman describes as 'breeding' and

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'settled', respectively; brown-capped woodpecker, *Picoides moluccensis* (fairly inconspicuous, but drumming); pied triller, *Lalage nigra*; magpie robin, *Copsychus saularis* (visually conspicuous, with loud song); mangrove whistler, *Pachycephala cinerea* (conspicuous); Phillipine glossy starling, *Aplonis panayensis* (social, with a loud whistle); brown-throated sunbird, *Anthreptes malacensis*; olive-backed sunbird, *Nectarinia jugularis* (conspicuous); and orange-bellied flower-pecker, *Dicaeum trigonostigma* (conspicuous), and we accept that these 14 species were absent in 1908. *Ducula bicolor* is regarded by Dammerman (1948) as one of a group of species, including sea and shorebirds, that although they breed there sometimes cannot be considered truly resident. There is no doubt that this is an in-and-out species, but we have accepted it as resident when recorded. In contrast, Dammerman accepts the great thick-knee, *Esacus magnirostris*, first seen in 1920 and a wide-ranging shorebird, as resident. Although conspicuous and frequently seen on the islands, and with evidence of breeding in 1951, we have not included this species as a resident land bird; we list it in table 3.

Three species may have been missed during Jacobson's short visit: the greater coucal, *Centropus sinensis*, crested goshawk, *Accipiter trivirgatus* and peaceful dove, *Geopelia striata*.

The greater coucal was heard, but not seen, by Bartels in 1919 on Sertung (an island only briefly visited by Jacobson in 1908) and has not been recorded since from the archipelago, and the only evidence of the presence of the peaceful dove during this survey period is a single specimen caught on Rakata by Bartels in 1919. The dove was recorded again in 1952 (see below). We accept both as being resident on the islands in the period 1919–22 and (on assessment) as having been missed by Jacobson (along with *A. trivirgatus*) in 1908.

Thus we accept 28 species present in 1919–1922 and probably resident. Additions during period II are thus on the records, 17, on assessment, 14; there were two losses. Maximum differences from 1908 are thus those accepting the records, +17 and −2 species, and minimum ones +14 and −2. We accept +14 and −2 for our calculations based on assessments (table 6).

Dammerman made short visits to the archipelago in July 1924 (three days on Rakata, one on Sertung). In February 1928 a visit of two days was made, during which Panjang was also investigated, and four species were recorded from this island for the first time; visits were made to Rakata and Sertung for three days in May 1929, and to Rakata, Sertung and the new island Anak Krakatau for three days in August 1930.

(iii) *Third survey*, 1932–1934 (*Dammerman*)

What may be called the second Dammerman survey lasted from 1932 to 1934, when, without an ornithologist, 14 days were spent on Rakata, 10 on Sertung and six on Panjang, and four visits were made to the new island Anak Krakatau (Dammerman 1948). These visits resulted in the recording of four additional resident land species: the large, striking Sunda Islands cuckoo-dove *Macropygia phasianella* (one specimen only, on Sertung), the white-bellied swiftlet *Collocalia esculenta* ('not seen during our earlier visits'), the flyeater, *Gerygone sulphurea* (common, unmistakeable song, first seen in 1928 on Sertung), and the mangrove blue flycatcher *Cyornis rufigastra* ('in great numbers and breeding', first seen in 1929). The cuckoo-dove was later found to be common and breeding on Rakata by Hoogerwerf. We accept all these as breeding residents in 1932–1934, and as absences in 1919–1922.

'Losses' included the long-tailed shrike, *Lanius schach*, which was numerous and breeding in 1919–1922, the greater coucal, *Centropus sinensis* and the peaceful dove, *Geopelia striata*.

On the records, 29 species were present in this survey period, and if the dove is assumed to have been missed by Dammerman's group the maximum number is 30. We use the maximum figure in our subsequent calculations based on assessments (table 6). Maximum species changes over the decade would be those according to the records: +4, −3, minimum changes +4, −2. We accept +4, −2 for our calculation based on assessments (counting the dove as having been present but missed in this survey).

(iv) *Fourth survey*, 1951–1952 (*Hoogerwerf*)

Hoogerwerf visited the archipelago for nine days in October 1951, spending most of the time on Rakata, briefly visiting the other islands. His 1952 visits were in August and November, to Anak Krakatau, for one day on each occasion, and and to Sertung for a few hours.

His surveys yielded six new records of resident land birds. Of these, five were present in fair numbers; the crested serpent-eagle, *Spilornis cheela* (heard frequently, but seen only once), silver-rumped swift, *Rhaphidura leucopygialis* (several specimens), black-naped fruit-dove *Ptilinopus melanospila* (frequent, monotonous call through most of year), scarlet sunbird, *Aethopyga mystacalis* (several, both sexes, two islands) and olive-winged bulbul, *Pycnonotus plumosus* (scattered groups, two islands). Hoogerwerf (1970*b*) recorded the black-naped fruit-dove, which ranges from Java to the east, on the Ujung Kulon peninsula more commonly after the Second World War than before, and Holmes (1977) recorded a pair on an island in Lampung Bay, Sunda Strait, in 1976. This dove was again found on the Krakataus in the 1980s, and it appears to have extended its range in the past few decades to include islands of Sunda Strait. We accept these as immigrants during intersurvey period IV that were absent in 1932–34, and assume breeding in 1951–52.

Only a single specimen of the oriental hobby, *Falco severus*, was seen, on Sertung, a month after the island's devastation by the November 1952 eruption of Anak Krakatau, but as we saw a pair on the latter island in 1986, we accept the 1952 record as evidence of residence. The peaceful dove, *G. striata*, unrecorded since 1919, was 'heard repeatedly' on Sertung on a visit of a few hours in 1952 (Hoogerwerf 1953*a*). Hoogerwerf knew the birds of the region well and we accept his record of this dove, and that it was resident, having been collected in 1919. Thus on records alone there were seven gains and on a conservative approach, six (if *G. striata* is assumed to have been present but missed during the third survey period).

Hoogerwerf pointed out that the three 'losses' noted by him should be treated with great caution in view of the limitations of his survey (nine days, mostly on parts of Rakata only). The species not recorded that had been present at the time of the previous survey included the crested goshawk, *Accipiter trivirgatus*, which Dammerman took to be a migrating besra (*Accipiter virgatus*) recorded during both his survey periods, but which Hoogerwerf believed was the former species. The other 'losses' were the pied imperial pigeon, *Ducula bicolor*, which, although conspicuous, is an in-and-out species, and *Hirundo tahitica*, the Pacific swallow, which was seen frequently on Rakata from 1919 to 1933. The goshawk has not been seen since on the islands, and we accept this as an extinction in 1951. *D. bicolor* is such an obvious species that we also accept its absence during Hoogerwerf's visit. *H. tahitica* was present during both of Dammerman's survey periods and also in the 1980s, and on the conservative approach we treat this as having been resident in 1951–52, but missed by Hoogerwerf.

Thus, on records, 33 species were present, the maximum number being 34. In subsequent calculations based on assessments (table 6) we use the maximum figure, regarding both *G.*

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striata and *H. tahitica* as being resident. The assumption of the miss of *G. striata* by Dammerman in 1932–34 after it had been recorded in the previous survey rests on the acceptance of Hoogerwerf's record in 1951–52 as evidence of residence. The combined assumption that Dammerman missed the species in 1932–34 when it was in fact present, and that Hoogerwerf recorded it in 1951–52 when it was not a resident, is considered to be too unlikely for acceptance. Gains and losses during intersurvey period IV are thus: on records +7, −3 (maximum), minimum +6, −2. We use +6, −2 in our second group of calculations (table 6).

(v) *Fifth survey*, 1984–86

So far as our own surveys are concerned (Zann *et al.* 1990*a*), we record seven gains and four losses, compared with Hoogerwerf's surveys.

The gains are *Ducula bicolor* (on all islands, but Anak Krakatau), the black eagle, *Ictinaetus malayensis* (seen in 1983 on Rakata and on all islands but Anak Krakatau in 1984–85, and a large, conspicuous species unlikely to have been missed by Hoogerwerf if present), green imperial pigeon, *Ducula aenea* (seen on all islands but Anak Krakatau in 1983 and on Rakata and Panjang in 1984–85), barn owl, *Tyto alba* (on all islands but Panjang), house swift, *Apus affinis* (on all islands), *Hirundo tahitica* (on all islands but Panjang), and the chestnut-capped thrush, *Zoothera interpres* (secretive, one individual taken on Rakata in 1984, another seen on Anak Krakatau in 1986).

In addition to these species, a single individual of the house crow, *Corvus splendens*, was seen, on Anak Krakatau in 1986, and two domestic fowls (both hens) were seen on Anak Krakatau in 1982 (Ibkar-Kramadibrata *et al.* 1986). The house crow had not been recorded previously, nor was it seen in the 1984 and 1985 surveys. A native of the Indian subcontinent, Sri Lanka and Thailand, it is not recorded from Java or Sumatra, although we saw it at Ujung Kulon in 1984. The house crow is a well-known human commensal that is a frequent passenger on ocean-going vessels (Ryall 1986) and sea traffic in Sunda Strait is heavy. The individual seen in 1986 flew on to our fishing boat at anchor, and stayed close to the camp kitchen; it was very tame and inquisitive. On the conservative approach of course we do not accept this as a resident population, although the species is currently expanding its range with the aid of sea traffic. Should other such incidents occur, the species may well become established. Domestic fowl were not encountered on any island during our 1984 or 1985 surveys, or in the 1986 intensive survey of the birds of Anak Krakatau. The species evidently did not become established in 1982. We do not count either of these species as resident birds, and list them in table 3.

Lynch & Johnson (1974) point out that 'absence of records of owls does not prove absence of the birds and verification of their presence is not necessarily proof of their residence'. We have no voucher specimen of the barn owl, but there is evidence of residence. In July 1982 the expedition of the Institute of Technology, Bandung, recorded the barn owl from Anak Krakatau (Ibkar-Kramadibrata *et al.* 1986), the record being based on calls (H. Ibkar-Kramadibrata, personal communication). A masked owl, later identified as the barn owl, was first observed, for some 10 min at a distance of four metres, on Rakata by I.W.B.T. in November 1982. Over a score of regurgitated pellets with rat bones and fur were found on Anak Krakatau in each of the years 1984, 1985 and 1986. An owl was seen fleetingly on the Sertung spit by I.W.B.T. and Sudarman in August 1985, and a pair of barn owls was seen, and heard almost nightly, on Anak Krakatau in September 1986. A primary feather collected in 1986 was matched to a barn owl skin in the Bogor Zoology Museum. The barn owl's colonization of the Karakataus would be consistent with its recent extension of range in the Sunda islands (Yaffle 1985), and the first record of the species in Sumatra (Lampung) in 1976 by Holmes (1977). Holmes thought the owl probably was already widespread in the open plains of Sumatra in 1977. Lenton (1983, 1984) has suggested that the owl's recent spread in peninsular Malaya is related to the high populations of rats, particularly *Rattus tiomanicus* on which the birds preferentially feed in oil palm estates. Both *Rattus rattus* and *R. tiomanicus* are present on the Krakataus. We believe the owl is a recent colonist and now a resident.

The secretive chestnut-capped thrush was taken in a mist-net on Rakata in September 1984. It is a true forest bird likely to become established on the archipelago late in the succession. Chasen (1937) remarked on its absence in the 1930s, it being known from Sebesi island, some 18 km to the north, in 1921. Surprisingly, we saw a specimen in the *Casuarina* woodland of Anak Krakatau in September 1986. We accept this as a resident, and as it was previously unrecorded from the island, accept its absence at the time of Hoogerwerf's visit.

Both *D. aenea* and *D. bicolor* have loud, far-reaching, characteristic calls, and the latter is also visually conspicuous; both are unlikely to have been missed by Hoogerwerf if present in 1952–52, and we believe them to be immigrants since then.

As we accept that Hoogerwerf may have missed *H. tahitica*, which was found in the previous and subsequent surveys, we do not count it as a gain in the 1980s in table 6. Thus the seven additional species recorded (discounting the house crow and *Gallus gallus*) (table 5) can be reduced to six on assessment (table 6).

Our 'losses' include *G. striata*, *E. scolopacea*, *S. cheela* and *R. leucopygialis*. We believe it unlikely that we would have missed the first three were they present in 1984 and 1985 (see Zann *et al.* 1990*a*), but do not count the swift (*R. leucopygialis*) as an extinction in table 6. Hoogerwerf saw this species from Rakata's 777 m summit, flying along the high northern cliff, and we accept that we may have missed it, although we investigated the summit area on several occasions. We believe that the large-billed crow, *C. macrorhynchos*, of which we saw a pair only, on Anak Krakatau, in 1984, became extinct before our 1985 and 1986 surveys (see below), but since it survived the intersurvey period, we count it as present. Extinctions may thus be counted as four on records alone (table 5), and three on assessment (table 6).

Differences from Hoogerwerf's survey are thus: on records, +7, −4 species (table 5), and on assessment (table 6) +6, −3.

(*b*) *Differences between the* 1984 *and* 1985 *data*

Results of our 1984 and 1985 surveys of resident land birds are summarized in table 4, which shows the effects that the slight differences in census numbers between the two years have on immigration and extinction figures when the censuses are considered separately and when they are combined.

'Gains' in 1985 compared with 1984 are the white-bellied swiftlet, *C. esculenta*, seen in large numbers on Rakata and Panjang, and which was present on Rakata in 1951–52 and 1932–34, and the pied triller, *L. nigra*, also seen on Rakata (twice, both sexes) and Panjang (once) in large casuarinas. The triller was recorded from Rakata and Sertung from 1919 to 1934 and from Rakata in 1951. We accept that both species could have been missed in 1984.

'Losses' between 1984 and 1985 include the brahminy kite, *Haliastur indus*, olive-winged

Table 4. Comparison of data from 1984 and 1985 surveys of resident land bird species on the Krakataus

	1984	1985	1984–1985 combined
number of species recorded	34	32	36
gains since 1951–52 (33 spp.)	5	5	6
losses since 1951–52 (33 spp.)	6	7	4
'gains' since 1984	—	2	—
'losses' since 1984	—	4	—
cumulative number of species	44	45	45

bulbul, *Pycnonotus plumosus*, chestnut-capped thrush, *Zoothera interpres*, and large-billed crow, *Corvus macrorhynchos*. The kite was seen high above Zwarte Hoek in 1984 and the site was only briefly visited in 1985; we believe the species may have been present also in 1985. Similarly, the thrush was caught at South Bay, Rakata, in 1984 after 1456 m^2 hours of mist-netting; in 1985 we only carried out 117 m^2 hours of mist-netting at South Bay, and this furtive species was very probably present in 1985. In 1986 an individual was seen in the *Casuarina* woodland of Anak Krakatau. The bulbul was seen in 1984 once on Sertung and once on Rakata but was not recorded in 1985. We believe it may still be present on the islands but, in contrast to the common yellow-vented bulbul, *Pycnonotus goiavier*, quite rare. We saw a pair of large-billed crows, *Corvus macrochynchos*, on each of three visits to Anak Krakatau in 1984 but the species, which is conspicuous, was not seen on any island in 1985 or 1986 and we believe it was absent. It may be regarded as an extinction since 1984. Differences between the 1984 and 1985 surveys are thus, on sightings +2, −4, and, conservatively, −1 species.

Thus, with minimal cryptoturnover in the one year between surveys, extinction rate is one species per year, about 3% of the standing fauna, a rate similar to that calculated for Krakatau birds at equilibrium by MacArthur & Wilson (1967).

(*c*) *Cryptoturnover and pseudoturnover*

The problem of cryptoturnover (species becoming extinct and re-immigrating within the intersurvey period; see Lynch & Johnson (1974)) during such long intersurvey periods is a difficult one, and examination of the slight differences between our 1984 and 1985 surveys (see above) does not help, re-immigrations cannot be scored in but two surveys.

Some estimate of pseudoturnover (inflated calculations of turnover based on spurious instances of immigration and extinction due to incomplete censuses; see Lynch & Johnson (1974) and Simberloff (1976)), however, can be made from such a comparison. Considering only the island of Rakata, on the evidence of presences and absences the resident land avifauna of 1985 shows +2 (*C. esculenta*, *L. nigra*) and −3 (*H. indus*, *P. plumosus*, *Z. interpres*) compared with that of 1984. We believe these differences are open to question (see §5*b*) and may represent pseudoturnover. If we are right in this, pseudoturnover is of the order of some 7% ($5/2 \times 100/34$) of the standing fauna of 34 species. Taking the archipelago as a whole, differences between our 1985 and 1984 surveys are +2 and −4 species, and we consider all but one (*C. macrorhynchos*) of these as representing pseudoturnover, that is, $5/2 \times 100/37$, 7% of the standing fauna of 37 species. Thus changes may have been overestimated in the past as a result of pseudoturnover by from 2 to 5 species at each survey. Put another way, we believe that 'real turnover' made up only a sixth of the 'observed turnover' between our surveys.

Such overestimates will almost certainly be more than compensated for by underestimates due to cryptoturnover, which must have been considerable because of the long intersurvey

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intervals and because Anak Krakatau's eruptions have affected the successional processes on at least Anak Krakatau, Sertung and Panjang, increasing the likelihood of species colonizing and becoming extinct between surveys.

By examining data from our 1984 and 1985 surveys (§5*b*) we minimized the possibility of cryptoturnover, assessed and discounted pseudoturnover, and measured actual extinction. If this single measure were representative, actual extinction rate during period V would be 1.00 species per year, ranging theoretically from 0.50 to 1.49 species per annum. Measured (apparent) extinction rate over this period (table 6) was 0.09 species per annum. Cryptoextinction rate, then, was 0.91 species per annum, ranging from 0.41 to 1.40 species per annum, some ten times the measured rate (see Jones & Diamond 1986).

(*d*) *Turnover on the archipelago*

Seventy-nine percent of immigrant species in the first half-century since 1883 are recorded from Singapore in a recent list by the Singapore Branch of the Malaysian Nature Society (Briffett 1986), showing the predominance of species of coastal scrub, mangrove, and open habitats. This is supported by an analysis of the successful colonists from potential pool areas (section §6*a*, below), which also shows that wide-ranging birds appear to be more successful than those with limited distributions.

Table 5 is based purely on the records for the archipelago. It shows immigration rate (I), the number of species of immigrants to the islands per year, extinction rate (E), the number of species becoming extinct per year, and colonization rate (C), the summation of these, that is, the net number of additional species, or in practical terms, the observed increase in species number per year (Whittaker *et al.* 1984), for the intersurvey periods since 1883.

Table 5. Turnover of resident land bird species on the Krakataus based on survey records

intersurvey period	I		II		III		IV		V	
survey date		1908		1919–21		1932–34		1951–52		1984–86
intersurvey interval (years)	25		12		13		18.5		33.5	
actual number of species		13		28		29		33		36
cumulative number of species		13		30		34		40		45
gains		13		17		4		7		7
losses		—		2		3		3		4
I (immigration rate)	0.52		1.42		0.31		0.38		0.21	
E (extinction rate)	—		0.17		0.23		0.16		0.12	
C (colonization rate)	0.52		1.25		0.08		0.22		0.09	
T (turnover rate)	0.26		0.79		0.27		0.27		0.16	
$\lambda_{\bar{s}}$ (acquisition rate coefficient) × 100	8.00		6.91		1.08		1.23		0.61	
$\mu_{\bar{s}}$ (extinction rate coefficient) × 100	—		0.81		0.81		0.52		0.35	
γ (colonization rate coefficient) × 100	8.00		6.10		0.27		0.71		0.26	
τ (turnover rate coefficient) × 100	4.00		3.86		0.94		0.88		0.48	
λ_{sp} (pool immigration rate coefficient*) × 100	0.33		0.98		0.23		0.28		0.16	

(*, With assumed pool of 165 species.)

Immigration rate reached a peak in period II (1908–1921), then fell sharply over the next decade, subsequently remaining steady at about one additional species every three to five years. Extinction rate peaked in intersurvey period III, the one following that in which immigration rate peaked; otherwise it is fairly constant at about 0.16 species per year. Colonization rate of course peaked with immigration rate, in period II (1908–1921), as did turnover rate.

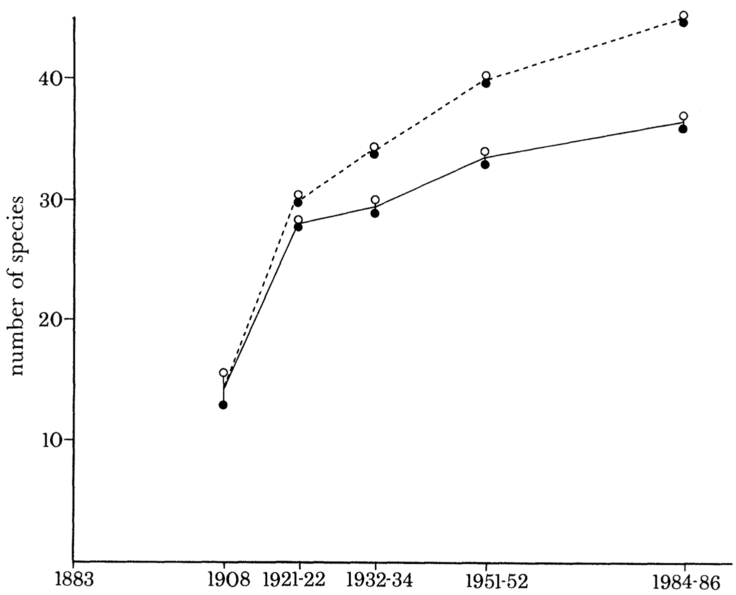

FIGURE 3. Colonization curve of resident land bird species, Krakatau Islands, based on data in tables 2, 5 and 6. Filled circles, on records; empty circles, on assessment; solid line, actual curve; dashed line, cumulative curve.

Table 6 sets out data based on the assessments of survey records made in §5*a*. In figure 3, the data of both tables 5 and 6 are represented. When the 'assessed' data are used, rather than the records themselves, only extinction rates are substantially affected, showing no peak in period III.

Coefficients of acquisition, colonization and turnover are highest in the first intersurvey period since 1883, when numbers were low, and there could be no extinctions recorded for this period. Actual immigration rate and colonization and turnover rates were highest in the second intersurvey period (1908 to 1919–21) when the forest were forming, and there were some extinctions on the records. Immigration rates fell during the third intersurvey interval

TABLE 6. TURNOVER OF RESIDENT LAND BIRD SPECIES ON THE KRAKATAUS BASED ON ASSESSMENTS OF SURVEY RECORDS

intersurvey period	I		II		III		IV		V	
survey date		1908		1919–21		1932–34		1951–52		1984–86
intersurvey interval (years)	25		12		13		18.5		33.5	
actual number of species		16		28		30		34		37
cumulative number of species		16		30		34		40		45
gains		16		14		4		6		6
losses		—		2		2		2		3
I (immigration rate)	0.64		1.17		0.31		0.32		0.18	
E (extinction rate)	—		0.17		0.15		0.11		0.09	
C (colonization rate)	0.64		1.00		0.15		0.22		0.09	
T (turnover rate)	0.32		0.67		0.23		0.22		0.13	
λ_s (acquisition rate coefficient) $\times$ 100	8.00		5.30		1.06		1.01		0.50	
μ_s (extinction rate coefficient) $\times$ 100	—		0.76		0.53		0.34		0.25	
γ (colonization rate coefficient) $\times$ 100	8.00		4.55		0.53		0.68		0.25	
τ (turnover rate coefficient) $\times$ 100	4.00		3.03		0.80		0.68		0.38	
λ_{sp} (pool immigration rate coefficient*) $\times$ 100	0.41		0.82		0.23		0.24		0.14	

(*, With assumed pool of 165 species.)

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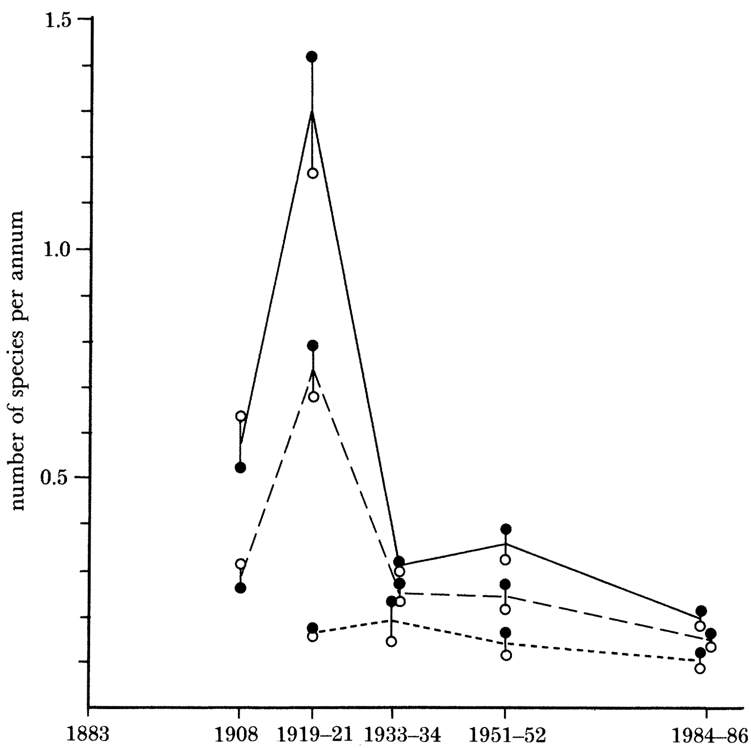

FIGURE 4. Turnover rates of resident land bird species, Krakatau Islands, at times of various surveys. Based on tables 5 and 6. Filled circles, on records; empty circles, on assessment; (—), immigration rate; (– –), turnover rate; (- - - -) extinction rate.

(figure 4) when the forest canopy was becoming closed, and remained at about the same level thereafter, but extinction rates changed little during the third intersurvey interval, gradually reducing since then.

Table 7 shows the percentages of immigrants of different habitats and eating different foods for the periods before and after forest formation. The differences are not striking, but the

TABLE 7. PERCENTAGES OF RESIDENT LAND BIRD SPECIES WITH VARIOUS FEEDING AND HABITAT PREFERENCES THAT COLONIZED THE KRAKATAUS BEFORE AND AFTER 1921

(Number of species in brackets. Feeding data from Smythies (1981), Hoogerwerf (1949*a*, *b*), and Frith (1976, 1982); habitat data from King *et al.* (1975) and Hoogerwerf (1970*b*).)

	1883–1921 (30)	1922–1986 (15)
feeding		
predators	17 (5)	27 (4)
specialist frugivores	10 (3)	20 (3)
facultative frugivores	20 (6)	7 (1)
insectivores	33 (10)	40 (6)
insectivores–granivores	7 (2)	0 (0)
granivores	3 (1)	0 (0)
omnivores	3 (1)	0 (0)
nectarivores–insectivores	7 (2)	7 (1)
habitat		
coasts, mangroves, open country	73 (22)	20 (3)
scrub, secondary growth	20 (6)	13 (2)
forests	7 (2)	67 (10)

percentage of predators increased, and there were proportionately more specialist and fewer facultative frugivores in the second period. Generally, there appears to be a change towards more specialist feeders in the second period, but the differences and the numbers are not great enough to warrant further comment. The percentage of immigrants that were true forest birds, however, increased very significantly, and the proportion of open country immigrants decreased. The only forest bird to have become established by 1908 was *Chalcophaps indica*, the green-winged pigeon. It prefers forest and shade, but is a ground feeder on fruits and insects, and in the absence of predators was able to colonize in the first 25 years. It is still on the islands, but has not yet colonized Anak Krakatau.

We believe the establishment of forest and closure of the canopy in the 1920s and 1930s are the events that have had the greatest effect on colonization parameters of resident land birds since 1883. This is of course a two-way relationship; Whittaker & Flenley (1982) believe that many forest plant species may have been brought in by birds at this time.

6. Equilibrium on the archipelago?

(*a*) *The mainland species pool*

All but three of the 45 resident land bird species known from the Krakataus have been recorded from both western Java and southern Sumatra (*F. severus*, *P. melanospila*, *Z. interpres* from Java only). Of the 42 species found on both sides of Sunda Strait, 16 have not been recorded from Barisan Selatan National Park, some 200 km west-northwest of the Krakataus. Only one species, *Tyto alba*, is found on the Krakataus and absent from Ujung Kulon (and Barisan Selatan) (table 8). Of 30 species collected on the Krakataus and identified to subspecies by Chasen (1937) and Hoogerwerf (1953*a*) three were Sumatran subspecies (*Pycnonotus goiavier*, *Copsychus saularis* and *Nectarinia jugularis*), two were Javan subspecies (*Cyornis rufigaster* and *Dicaeum trigonostigma*) and the remaining 25 subspecies were the same for both islands.

West Java, although much more densely populated than southern Sumatra, nevertheless has areas, sheltered from human development, in which the avifauna has been studied for several decades. The birds of the Cibodas area, an upland reserved region of west Java some 150 km from the west coast, have been described (Hoogerwerf 1949*b*), but the Ujung Kulon peninsula, which together with the Krakataus constitutes the Ujung Kulon National Park, has one of the best studied avifaunas in Indonesia (Hoogerwerf 1953*b*, 1970*b*).

The Ujung Kulon peninsula is well positioned to act as a source area for the Krakataus, being some 45 km to the southeast. Although before the 1883 eruption it was subjected to some shifting cultivation in the lowlands, it has not been occupied since then, when the coastal lowlands were inundated by tsunami (Hommel & van Reuler 1983) and rendered unsuitable for agriculture. Ash from the 1883 events also affected the peninsula, but to a relatively slight extent compared with the Krakataus themselves and the island of Sebesi to their north (which otherwise would have made an ideal 'control' island against which to measure the recolonization of the Krakataus). In 1921 the opportunity was taken to create a peninsular reserve at Ujung Kulon for the remaining population of Javan rhinoceros. The peninsula includes hills of a similar elevation to Rakata, has undoubtedly been an important source for recolonization by plants and is by far the closest undisturbed wilderness area to the archipelago.

Hoogerwerf (1970*b*) recorded 157 bird species from the peninsula that were not sea birds,

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water birds, migrants, or coastal stragglers, and a further six were recorded more recently (Blower & van der Zon 1977) and two more were noted by us. We regard these 165 species as the mainland pool, for the purpose of discussion.

Nineteen families listed in table 8 and three more known from other areas adjacent to Sunda Strait have never been represented on the Krakataus. Five additional families, the grebes, cormorants, storks, ducks and jacanas, would not have become established had dispersal been successful, for the archipelago contains virtually no natural bodies of fresh water. These have been excluded from the available pool figure (and table 8) because fresh water habitat is unlikely to become available on the islands in the future.

The proportion of the 165 Ujung Kulon species, which constitute the theoretical available pool, that makes up the effective available pool will vary with ecological conditions on the Krakataus.

Seven families absent from the Krakataus, parrots, hornbills, barbets, pittas, leafbirds, nuthatches and babblers are forest birds. Although the proportion of forest birds among Krakatau's immigrants has greatly increased since 1921 when the islands' forests began to take form (table 7), Hoogerwerf (1970*b*) records the presence on the Ujung Kulon peninsula of 18 species that he found only in 'heavy forest', and none of these has ever been found on the Krakataus, although four (a thrush, kingfisher, flycatcher and woodpecker) are on Panaitan Island (table 8). Babblers are poor fliers, and hornbills require mature forest with hollow trees for nesting. Barbets and leafbirds are birds of the treetops, the former being tree-hole nesters; nuthatches are trunk specialists. Pittas and babblers are birds of deep rainforest, pittas are ground birds and many babblers inhabit thick undergrowth. Pittas, barbets and babblers are absent from Simeulue and Siberut islands about 100 km off the west coast of Sumatra, and nuthatches are absent from Siberut and hornbills from Simeulue (Mitchell 1981; Anonymous 1980). Although clearly not very vagile, it is possible that the barrier to colonization of the Krakataus by these families is also ecological, the Krakatau forests not yet having reached the appropriate stage of maturity, although the fruit-eating parrots would have found several fig species since the 1920s.

Barbets, pittas and babblers are important components of tropical forest avifaunas (57 species occur throughout adjacent mainland forests), and if they continue to fail to colonize as the forest matures, the effect of their absence both on the forest itself and on the niches of other species of birds will be questions of considerable ecological interest.

Three families absent from the Krakataus, buttonquails, dollarbirds and grassfinches, comprise birds of grassland and open habitats that would have found the vegetation of the archipelago at an appropriate successional stage early in this century. Buttonquails, grassland birds, are poor reluctant fliers and absent from Simeulue and Siberut, but dollarbirds, found in open country, and grassfinches, which feed on grass seeds, may have been expected to colonize the islands during the grassland phase of succession (dollarbirds occur on Simeulue and Siberut, but grassfinches do not). This phase, however, was relatively short, and once having missed the opportunity they would not be expected to establish themselves after the 1920s when the secondary forest canopy began to close.

A preliminary list of birds from Barisan Selatan National Park in southern Sumatra some 200 km W.N.W. of the Krakataus includes 86 resident land birds (de Wulf *et al.* 1981) and Davison, on our 1984 expedition, recorded another 35. Of the 121 species now recorded from the park (table 8) 26 are known from the Krakataus, but of the 59 that have never been

TABLE 8. LIST OF RESIDENT LAND BIRDS FOR UJUNG KULON PENINSULA (UK), BARISAN SELATAN NATIONAL PARK (BS), THE KRAKATAUS, PANAITAN AND SEBESI

(Data for Ujung Kulon from Hoogerwerf (1970*b*), Blower & van der Zon (1977) and Zann (unpublished); data for Baritan Selatan from de Wulf *et al.* (1981) and G. Davison unpublished data; the Panaitan list is from Hoogerwerf (1953*a*, *b*) and Sebesi data from Chasen (1937) and Dammerman (1923). J, Javan subspecies; S, Sumatran subspecies; JS, same subspecies on Java and Sumatra (Chasen 1937; Hoogerwerf 1953*a*); ×, not identified to subspecies. Names according to King *et al.* (1975), MacKinnon (1988) and van Marle & Voous (1988).

	UK	BS	Krakataus	Panaitan	Sebesi
Pandionidae					
Pandion haliaetus	×	×	—	×	—
Accipitridae					
Pernis apivorus	×	—	—	—	—
Elanus caeruleus	×	—	—	—	—
Haliastur indus	×	×	JS	×	×
Haliaeetus leucogaster	×	×	JS	×	×
Icthyophaga ichthyaetus	×	×	—	×	—
Spilornis cheela	×	×	JS	×	—
Accipiter trivirgatus	×	×	×	—	—
Butastur liventer	×	—	—	—	—
Ictinaetus malayensis	×	×	×	—	—
Spizaetus cirrhatus	×	×	—	—	—
Falconidae					
Falco moluccensis	×	—	—	—	—
F. severus	×	—	JS	—	—
Phasianidae					
Coturnix chinesis	×	—	—	—	—
Gallus gallus	×	×	—	×	—
G. varius	×	—	—	—	—
Argusianus argus	—	×	—	—	—
Pavo muticus	×	—	—	—	—
Turnicidae					
Turnix suscitator	×	—	—	×	—
Rallidae					
Rallus striatus	×	—	—	—	—
Porzana fusca	×	—	—	×	—
P. cinerea	—	×	—	—	—
Amaurornis phoenicurus	×	—	JS	×	×
Columbidae					
Treron griseicauda	×	—	—	×	—
T. vernans	×	×	JS	×	×
T. capelli	—	×	—	—	—
Ptilinopus melanospila	×	—	J	×	—
Ducula aenea	×	×	×	×	—
D. bicolor	×	×	×	—	×
Macropygia phasianella	×	—	JS	×	—
M. unschall	—	×	—	—	—
M. ruficeps	×	—	—	—	—
Streptopelia bitorquata	×	—	—	×	—
S. chinesis	×	×	—	—	—
Geopelia striata	×	—	JS	×	—
Chalcophaps indica	×	×	JS	×	×
Psittacidae					
Psittacula alexandri	×	—	—	—	—
Psittinus cyanurus	—	×	—	—	—
Loriculus vernalis	×	—	—	—	—
L. galgulus	—	×	—	—	—
Cuculidae					
Cuculus micropterus	×	—	—	—	—
C. saturatus (= *poliocephalus*)	×	—	—	—	—
Cacomantis sonneratii	×	—	—	—	—

TABLE 8. (*cont.*)

	UK	BS	Krakataus	Panaitan	Sebesi
Cuculidae (*cont.*)					
C. merulinus	×	×	—	—	×
C. variolosus	×	—	—	—	—
Chrysococcyx xanthorhynchus	—	×	—	—	—
C. minutillus (=*malayanus*)	×	—	—	—	—
Surniculus lugubris	×	—	—	—	—
Eudynamys scolopacea	×	×	JS	×	×
Phaenicophaeus diardi	—	×	—	—	—
P. javanicus	×	—	—	—	—
P. curvirostris	×	×	—	—	—
Centropus nigrorufus	×	—	—	—	—
C. sinensis	×	—	×	×	×
C. bengalensis	×	×	JS	—	×
Strigiformes					
Tyto alba	—	—	×	—	—
Otus bakkamoena	×	—	—	×	—
Ketupa ketupu	×	—	—	—	—
Ninox scutulata	×	—	—	—	—
Strix seloputo	×	—	—	—	—
Caprimulgidae					
Eurostopodus temminckii	—	×	—	—	—
Caprimulgus macrurus	×	—	—	×	—
C. affinis	×	—	JS	—	×
Apodidae					
Collocalia fuciphaga	×	×	×	×	—
C. esculenta	×	×	×	×	×
Hirundapus giganteus	×	—	—	—	—
Rhapidura leucopygialis	×	×	JS	—	—
Apus affinis	×	—	×	×	—
Cypsiurus batasiensis	×	—	—	×	—
Hemiprocnidae					
Hemiprocne comata	—	×	—	—	—
H. longipennis	×	×	—	×	—
Trogonidae					
Harpactes orrhophaeus	—	×	—	—	—
Alcedinidae					
Alcedo caerulescens	×	—	×	—	—
A. meninting	×	—	—	×	—
A. euryzona	—	×	—	—	—
Ceyx erithacus (= *rufidorsum*)	×	—	—	×	—
Pelargopsis capensis	×	×	—	×	—
Lacedo pulchella	×	—	—	—	—
Halcyon smyrnensis	—	×	—	—	—
H. coromanda	×	—	—	×	—
H. chloris	×	×	JS	×	×
H. cyanoventris	×	—	—	×	—
Meropidae					
Merops leschenaulti	×	—	—	—	—
M. viridis	×	×	—	—	—
Nyctyornis amictus	—	×	—	—	—
Coraciidae					
Eurystomus orientalis	×	—	—	—	—
Bucerotidae					
Rhyticeros undulatus	×	×	—	×	—
Anthracoceros malayanus	—	×	—	—	—
A. coronatus (= *convexus*)	×	×	—	×	—
Buceros rhinoceros	×	×	—	—	—
Rhinoplax vigil	—	×	—	—	—

TABLE 8. (*cont.*)

	UK	BS	Krakataus	Panaitan	Sebesi
Capitonidae					
Megalaima javensis	×	—	—	—	—
M. lineata	×	—	—	—	—
M. chrysopogon	—	×	—	—	—
M. mystacophanos	—	×	—	—	—
M. australis	×	×	—	×	—
M. haemocephala	×	—	—	—	—
Indicatoridae					
Indicator archipelagicus	—	×	—	—	—
Picidae					
Sasia abnormis	×	×	—	—	—
Micropternus brachyurus	—	×	—	—	—
Picus vittatus	×	—	—	—	—
P. flavinucha	—	×	—	—	—
P. puniceus	—	×	—	—	—
P. miniaceus	×	—	—	—	—
Dinopodium javanense	×	×	—	—	—
Meiglyptes tukki	—	×	—	—	—
Mulleripicus pulverulentis	×	×	—	×	—
Dryocopus javensis	×	—	—	×	—
Picoides moluccensis	×	—	JS	×	×
Blythipicus rubiginosus	—	×	—	—	—
Chrysocolaptes validus	×	—	—	—	—
Eurylaimidae					
Eurylaimus javanicus	—	×	—	—	—
E. ochromalus	—	×	—	—	—
Pittidae					
Pitta sordida	×	—	—	—	—
P. guajana	×	—	—	—	—
Hirundinidae					
Hirundo tahitica	×	×	×	—	×
H. daurica	×	—	—	—	—
Campephagidae					
Hemipus hirundinaceus	×	×	—	—	—
Coracina novaehollandiae	×	—	—	×	—
C. striata	—	×	—	—	—
Lalage nigra	×	—	JS	×	×
Pericrocotus cinnamomeus	×	—	—	×	—
P. flammeus	×	×	—	—	—
Chloropseidae					
Aegithina viridissma	—	×	—	—	—
A. tiphia	×	—	—	—	—
Chloropsis venusta	—	×	—	—	—
C. cyanopogon	—	×	—	—	—
C. sonnerati	×	—	—	—	—
C. cochinchinensis	×	—	—	—	—
Pycnonotidae					
Pycnonotus zeylanicus	×	×	—	—	—
P. atriceps	×	—	—	×	—
P. melanicterus	×	×	—	—	—
P. aurigaster	×	×	×	—	—
P. eutilotus	—	×	—	—	—
P. goiavier	×	×	S	×	×
P. plumosus	×	×	JS	×	—
P. simplex	×	×	—	—	—
P. brunneus	—	×	—	—	—
Criniger ochraceus	—	×	—	—	—
C. bres	×	—	—	—	—
C. phaeocephalus	—	×	—	—	—
Hypsipetes criniger	—	×	—	—	—

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TABLE 8. (*cont.*)

	UK	BS	Krakataus	Panaitan	Sebesi
Dicruridae					
Dicrurus macrocercus	×	—	—	—	—
D. aeneus	—	×	—	—	—
D. remifer	—	×	—	—	—
D. hottentottus	×	—	—	×	—
D. paradiseus	×	×	—	—	—
Oriolidae					
Oriolus chinensis	×	—	JS	×	×
Irena puella	×	×	—	—	—
Corvidae					
Platylophus galericulatus	—	×	—	—	—
Crypsirina temia	×	—	—	—	—
Platysmurus leucopterus	—	×	—	—	—
Corvus splendens	×	—	—	—	—
C. macrorhynchus	×	×	JS	—	×
C. enca	×	×	—	×	—
Sittidae					
Sitta frontalis	×	×	—	—	—
Timaliidae					
Pellorneum capistratum	×	—	—	—	—
Trichastoma malaccense	—	×	—	—	—
T. bicolor	—	×	—	—	—
T. sepiarium	×	—	—	—	—
Aethostoma pyrrhogenys	×	—	—	—	—
Malacopteron cinereum	×	—	—	—	—
M. magnum	—	×	—	—	—
Pomatorhinus montanus	—	×	—	—	—
Naptothera macrodactyla	×	—	—	—	—
Stachyris grammiceps	×	—	—	—	—
S. melanothorax	×	—	—	—	—
S. nigriceps	—	×	—	—	—
S. poliocephala	—	×	—	—	—
Macronous gularis	×	×	—	—	—
M. kelleyi	×	—	—	—	—
M. ptilosus	—	×	—	—	—
Timalia pileata	×	—	—	—	—
Alcippe brunneicauda	—	×	—	—	—
Turdidae					
Copsychus saularis	×	×	S	×	—
C. malabaricus	×	×	—	×	×
Enicurus ruficapillus	—	×	—	—	—
E. leschenaulti	×	—	—	—	—
Zoothera interpres	×	—	×	—	×
Z. citrina	×	—	—	—	—
Sylviidae					
Gerygone sulphurea	×	—	JS	×	—
Orthotomus sutorius	×	×	—	—	—
O. atrogularis	—	×	—	—	—
O. ruficeps	×	×	—	×	×
Prinia familiaris	×	—	—	—	—
P. subflava	×	—	—	—	—
P. flaviventris	—	×	—	—	—
P. polychroa	×	—	—	—	—
Cisticola juncidis	—	×	—	—	—
C. exilis	×	—	—	×	—
Muscicapidae					
Cyornis rufigastra	×	×	J	—	×
C. banyumas	×	—	—	×	—
Culicicapa ceylonensis	—	×	—	—	—
Rhipidura perlata	—	×	—	—	—

TABLE 8. (*cont.*)

	UK	BS	Krakataus	Panaitan	Sebesi
Muscicapidae (*cont.*)					
Rhipidura javanica	×	—	—	×	—
Hypothymis azurea	×	×	—	×	—
Philentoma velatum	×	—	—	—	—
Terpsiphone paradisi	×	×	—	—	—
Pachycephalidae					
Pachycephala cinerea	×	—	JS	×	×
Motacillidae					
Anthus novaeseelandiae	×	×	—	—	—
Artamidae					
Artamus leucorhynchus	×	—	JS	×	×
Laniidae					
Lanius schach	×	—	×	—	—
Sturnidae					
Aplonis panayensis	×	×	JS	×	×
Sturnus contra	×	—	—	—	—
Acridotheres javanicus	×	—	—	—	—
Gracula religiosa	×	×	—	×	—
Nectariniidae					
Anthreptes simplex	—	×	—	—	—
A. malacensis	×	×	JS	×	×
A. singalensis	×	—	—	—	—
Nectarinia sperata	×	—	—	—	—
N. jugularis	×	×	S	×	×
Aethopyga siparaja	×	—	—	×	—
A. mystacalis	×	—	×	—	—
Arachnothera longirostra	×	×	—	×	×
A. robusta	—	×	—	—	—
A. affinis	×	—	—	—	—
Dicaeidae					
Dicaeum trigonostigma	×	×	J	×	×
D. trochileum	×	—	—	×	—
D. cruentatum	—	×	—	—	—
Ploceidae					
Passer montanus	—	×	—	—	—
Erythrura prasina	×	—	—	×	—
Padda oryzivora	×	—	—	—	—
Lonchura leucogastra	×	×	—	—	—
L. punctulata	—	—	—	—	×
L. malacca	—	×	—	—	—
L. maja	—	×	—	—	—
Total	165	121	45	66	31

TABLE 9. NUMBER OF SPECIES OF RESIDENT LAND BIRDS RECORDED FROM THE UJUNG KULON (UK) AND BARISAN SELATAN (BS) NATIONAL PARKS THAT HAVE COLONIZED THE KRAKATAUS

(UK data from Hoogerwerf (1970*b*), Blower & van der Zon (1977) and our own observations; BS data from de Wulf *et al.* (1981) and G. Davison's unpublished observations in 1984.)

	UK only	UK and BS	BS only	total
species present	103	62	59	224
species recorded from Krakataus	18	26	0	44
percentage recorded from Krakataus	17	42	0	20
percentage of Krakataus fauna	40	58	0	98

recorded from Ujung Kulon not one has become established on the islands. Of the 165 resident land bird species known from Ujung Kulon, 103 are not recorded from Barisan Selatan, and 18 of these are known from the Krakataus. Sixty-two species are found in both areas and of these 26 (42%) have colonized the Krakataus. The babblers (family Timaliidae, table 8) are a striking example of this tendency. Nine species occur in Barisan Selatan and ten in Ujung Kulon on Java; only one species occurs in both areas, and none has ever been recorded from the Krakataus. These data support the suggestion made above that the Krakataus have been colonized predominantly by wide-ranging birds or birds with rather wide ecological tolerances.

Our theoretical pool of 165 Ujung Kulon species already discounts all water birds, which clearly lack habitat on the Krakataus. A closer estimate of the effective pool over the last century may be made by also discounting seven Ujung Kulon families of mature forest birds (25 species) that have not colonized the islands and still lack appropriate habitat, leaving 140 species.

An estimate of the effective pool may also be made by using the colonization data in table 6. In §6*c* we fit equation 1 to this data to obtain an estimate of $\hat{S}$ (36 species), and obtain a value of 18.3 years for t_r, the time for the difference from equilibrium to reduce to 36.8% (e^{-1}) of the initial difference (Diamond 1972). Diamond showed that $1/t_r = \lambda_{sp} + \mu_{\bar{s}}$ (in our case = 0.055 per annum). Substituting for $\lambda_{sp} + \mu_{\bar{s}}$ and $\hat{S}$ in equation 13, $\lambda_{sp} \times P = 36 \times 0.055 = 1.980$ species per year. In §5*c*, by accounting for pseudoturnover and reducing cryptoturnover to near zero by comparing the surveys of 1984 and 1985, we estimate actual extinction rate as 1 species per annum, with a theoretical range of from 0.50 to 1.49 species per annum. Thus $\mu_{\bar{s}}$ ($= E/\bar{S}$) is 1/35.5 (§5*b*) = 0.028 per annum, ranging from 0.014 to 0.042 per annum. Since $\lambda_{sp} + \mu_{\bar{s}} = 0.055\ \mathrm{a}^{-1}$, $\lambda_{sp} = 0.027$, with a range of 0.041 to 0.013 a^{-1}. From $\lambda_{sp} \times P = 1.980$ species a^{-1}, $P = 73$ species (range 48–152 species). The estimated effective pool of 140, above, lies within this range, as does what is probably the 'hard core' of potential colonists, the 62 species common to both Ujung Kulon and Barisan Selatan (table 9).

Thus our minimal assumption, that the 165 resident land bird species of Ujung Kulon constitute the theoretical pool for the Krakataus, is not invalidated by the data; it is not necessary to postulate larger pools, such as the total of 224 species in Ujung Kulon and Barisan Selatan national parks combined or the more than 400 species in western Java and southern Sumatra (Mackinnon 1988; van Marle & Voous 1988).

(*b*) *The effect of the emergence of Anak Krakatau*

Anak Krakatau suffered a devastating eruption in 1952 (Hoogerwerf 1953*a*; van Borssum Waalkes 1954, 1960) and several damaging ones since then; the biota is thus no more than about three decades old. Grassy areas and a *Casuarina* association comprise the 5% (14 hectares†) of its area that is vegetated (figure 1). These were early successional stages on the three older islands, which are now covered in secondary forest.

Twenty-four resident land bird species have been recorded on the island since 1951–52, an acquisition rate of 0.72 species per annum, similar to the rate for the other islands in the 38 years after 1883 (0.74 species per year). This is in spite of the very small vegetated area available for colonization on Anak Krakatau, although to balance this, Anak Krakatau is much closer to potential sources (the three older islands) than were they at the time of their recolonization.

† 1 hectare = $10^4\ \mathrm{m}^2$.

Some birds of open country are now absent from (white-breasted waterhen) or rare (savannah nightjar, lesser coucal) on the other islands, where open habitats have now been extirpated by vegetational succession apart from small areas of Sertung on its northern spit (figure 1), which, like Anak Krakatau, is physically (Rosengren 1985) and successionally young. The Sertung spit and Anak Krakatau would provide ecological refuges for such species, provided the birds could persist on other islands until their diminishing preferred habitat became available on Anak Krakatau. The spit may not persist but, volcanic activity permitting, Anak Krakatau may long continue to rescue such species from extinction on the archipelago. Twenty (74%) out of the 27 resident land species now present that became established on the archipelago by 1934, before Anak Krakatau provided a habitat for land birds, are now found on Anak Krakatau and make up 83% of its resident land bird fauna, and nine (90%) out of the 10 species surviving on the archipelago that colonized by 1908 are now on the island (table 10). In contrast, of the 10 survivors that became resident on the island group since 1934, only four (40%) are now on Anak Krakatau, making up the remaining 17% of its resident land bird fauna.

TABLE 10. REPRESENTATION ON KRAKATAU ISLANDS IN THE 1980S OF SURVIVING RESIDENT LAND BIRD SPECIES FIRST ARRIVING ON THE ARCHIPELAGO AT DIFFERENT TIMES SINCE 1883

(Percentages in brackets. R, Rakata; S, Sertung; P, Panjang; A, Anak Krakatau.)

years since 1883	survey dates	species assessed as first resident in previous intersurvey period	number (%) recorded on Krakatau islands in 1980s			
			R	S	P	A
25	1908	10	9 (90)	9 (90)	9 (90)	9 (90)
36–38	1919–21	13	11 (85)	9 (69)	9 (69)	8 (62)
49–51	1932–34	4	4 (100)	3 (75)	4 (100)	3 (75)
68–69	1951–52	5	5 (100)	1 (20)	2 (40)	1 (20)
101–103	1984–86	5	5 (100)	4 (80)	3 (60)	3 (60)

The island's provision of younger habitats on the archipelago may also have allowed the augmentation from the mainland of island populations that were declining as a result of habitat reduction by vegetational succession, a 'rescue effect' in the sense of Brown & Kodric-Brown (1972). The emergence of Anak Krakatau has thus probably resulted in a postponement of the extinction of birds already present on the archipelago

The island's emergence has also reopened a successional 'window' to some mainland species that on the other islands has been closed, thus increasing the chances of colonization of those that failed to take the opportunity earlier in the century, or the recolonization of those that may have become extinct as a result of successional extirpation of habitat. Although a migrant, the tiger shrike (*Lanius tigrinus*), one individual of which was netted on Anak Krakatau in 1986, may illustrate this effect; certainly shrikes are birds of open habitats, although *L. tigrinus* is unusual in its apparent preference for woodland (King *et al.* 1975). If, as we believe, the barn owl is a recent colonist, its success may be due to the re-availability of open habitats on Sertung and Anak Krakatau.

These effects may continue until Anak Krakatau's vegetation becomes the last on the archipelago to come into equilibrium. Hence, Anak Krakatau's emergence will result in reduction of turnover, a delay in the achievement of equilibrium in bird species on the archipelago, and a slightly higher equilibrium number of species because of the gradually increasing area of habitat.

(*c*) *The equilibrium number*

Assuming that the mainland pool for the island group is 165 species, and using the latest inter-survey interval (the most appropriate, as immigration and extinction rates have not been constant since 1883), the equilibrium number of species ($\hat{S}$) on the Krakataus may be calculated (MacArthur & Wilson 1967) from the equation:

$$\hat{S} = \lambda_{sp} P/(\mu_{\bar{s}} + \lambda_{sp}). \tag{13}$$

By using data from table 5 (unadjusted records) for period V,

$$\lambda_{sp} = \frac{7}{33.5} \times \frac{1}{16(5) - 34.5} = 0.0016 \text{ per year,}$$

(0.16 % of the available pool per year), and

$$\mu_{\bar{s}} = \frac{4}{33.5} \times \frac{1}{34.5} = 0.00346 \text{ per year,}$$

(0.35 % of the standing fauna per year).

By using data from table 6 (assessed records), λ_{sp} is 0.0014, and $\mu_{\bar{s}}$ 0.0025.

Thus by using equation (13) $\hat{S}$ (equilibrium number of species) would be:

$$\frac{0.00160 \times 165}{0.00506} \text{ (52 species) or } \frac{0.00138 \times 165}{0.00391} \text{ (58 species).}$$

We have counted the large-billed crow in our 1984–86 tallies, both of unadjusted records and on assessed records, on the grounds that it survived to the beginning of our survey period. However we believe it may have become extinct during our survey, and if this is so one could take the view that it did not survive the total period, that is, including the years in which we surveyed. If the crow is discounted, the calculated equilibrium numbers of species using unadjusted and assessed records fall to 44 and 47, respectively, and extinction rate increases to about 0.4 % of the fauna per year (about one species every seven or eight years).

By using the above methods with a small fauna, a change in the accepted number of resident species of even one species greatly perturbs the value of λ_{sp} and $\mu_{\bar{s}}$. Moreover, the method incorporates errors due to cryptoturnover.

If cryptoturnover is accounted for, equation 1 (§4*a*) becomes $\lambda_{sp} = (I+x)/(P-S)$ and equation (4) $\mu_{\bar{s}} = (E+x)/S$, where x = cryptoimmigration rate = cryptoextinction rate. By using equation (13) the ratio $\hat{S}_a/\hat{S}_b$ can be investigated, where $\hat{S}_a$, $\hat{S}_b$ are equilibrium numbers calculated from data for period V (table 6) by using measured ($\hat{S}_a$) and actual (measured + crypto-) turnover ($\hat{S}_b$):

$$\frac{\hat{S}_a}{\hat{S}_b} = \frac{1 + (x/I) + [(P/\bar{S}) - 1]\,[(E/I) + (x/I)]}{[1 + (x/I)]\,\{1 + (E/I)\,[(P/\bar{S}) - 1]\}} \tag{14}$$

$P/\bar{S}$ (165/35.5) and E/I (0.09/0.18) are known (table 6), as is x/I (0.91/0.18) (§5*c* and table 6). By substitution, $\hat{S}_a/\hat{S}_b$ is 1.54, i.e. correcting for cryptoturnover reduces the prediction of $\hat{S}$ from 58 to 37.7 (38) species.

$\hat{S}$ may be estimated by another method, independent of I, E or C, by fitting through all the data points the equation:

$$S(t) = \hat{S}[1 - \exp - (t - t_0)/t_r], \tag{15}$$

where $S(t)$ = number of species at time t, t = time from 1883, and t_0 = time from 1883 to beginning of colonization. This reduces to Diamond's (1972) equation 6 for $t_0 = 0$, i.e. colonization began at the time of eruption. In fitting the equation we made the following provisions: (i) the curve must pass through the theoretical ranges of data for surveys with ornithologists (1920.4*, 27.50–28.49; 1951.8, 32.50–34.49; 1985.2*, 35.50–37.49); (ii) it must not pass below the data, regarded as minimal estimates, for surveys lacking ornithologists (1908.4, 16+; 1932.9*, 30+). Asterisks show means of dates of closely grouped surveys, weighted for survey durations. Equation 15 satisfies these conditions for $t_0 = 10.3$ years, $t_r = 18.3$ years, and $\hat{S} = 36$ species, close to the corrected value obtained above.

The above values for $\hat{S}$ compare with previous estimates of about 30 (MacArthur & Wilson 1967) and 40–45 species (Mayr 1965).

The number of species of resident land birds is approaching an equilibrium higher than that estimated by MacArthur & Wilson; the 1919–24 number evidently represents not equilibrium but a point after which the rate of increase sharply declined (figure 3). This pattern is repeated in the data for reptiles (Rawlinson *et al.* 1990), and the rate of increase of vascular plant species on Rakata also declined from this time, which was when canopy closure began (Whittaker *et al.* 1984).

Increase in resident land bird species (totalling 25%) since 1921 is about one every four years, compared with about one every 15 months previously. Measured extinction rates for long intersurvey periods since 1934 (tables 5 and 6) vary from 0.09 to 0.16 species per year, 0.25–0.52% of the standing fauna. These ranges are an order of magnitude lower than the annual extinction rates (from 0.5 to 1.6 species per year and from 2 to 6% of the standing fauna) estimated by MacArthur & Wilson (1963) from the data up to 1934. The birth of Anak Krakatau in 1930 and its subsequent provision of habitat at a younger successional stage than that generally occurring on the older islands may partly account for this difference (see §6*b*), although cryptoturnover during long intersurvey intervals is probably the main reason. When this was minimized by annual surveys, extinction rate (1.00 species per year, 2.82% of the fauna) was within the range calculated by MacArthur & Wilson (1963) (§5*b*).

(*d*) *Species–area considerations*

The relation between the number of species occurring on an island and the island's area is well established in island biogeography theory (MacArthur & Wilson 1967) as conforming to equation $S = CA^z$, and it is of interest to examine this relation for the islands in the Sunda Strait that have been surveyed for birds (the Krakataus, Sebesi and Panaitan, see figure 1). The Ujung Kulon peninsula, believed to be a major source of immigrants to the Krakataus, might also be considered as an island and included in the analysis.

The relation applies to islands that have achieved an equilibrium number of species, and the value of z (the gradient of the log versus log plot of the species–area curve) has been found, for various taxa and island situations, to lie between 0.20 and 0.35 (0.20–0.35, MacArthur & Wilson 1967; 0.24–0.34, Gorman 1979). Table 11 shows the values of z obtained for various combinations of the Sunda Strait islands and Ujung Kulon, for resident land birds.

There are several complications in attempting this exercise; the data set is 'untidy' in a number of respects. The application of the known data on Sebesi is questionable; the islands and Ujung Kulon are at different stages of the approach to equilibrium after the 1883 event; Anak Krakatau, a new island, is at a very early stage of colonization and its 'effective area' is open to interpretation; and of course Ujung Kulon is not an island.

Sebesi was partly devastated in 1883 (Dammermann 1923) and it is unlikely that the 31 species found there in 1920–22 represent the number present now, over six decades later. Thirty-one is regarded as a seriously out-dated underestimate of the island's species number, and the island is omitted from the analysis in table 11. Data for the other areas are more recent, although those of Panaitan are over three decades old.

Including Ujung Kulon in the analysis, and taking the area of Anak Krakatau as 2.8 km^2 (its actual area), z is 0.37, rather higher than the published range cited above. If the effective area of Anak Krakatau is taken as 0.14 km^2 (the vegetated area of the island, the vast tracts of ash and lava being considered as equivalent to sea as far as resident land birds are concerned) the value of z drops to 0.24 (near the bottom of the published range).

The Ujung Kulon peninsula is connected to mainland Java by a low, narrow neck of land (that was inundated by tsunami in 1883) and its species number may be expected to be greater than would be the case were it truly insular. The peninsula was relatively unaffected in 1883, most of the long-term devastation being in low-lying coastal areas as a result of tsunami (Hommel & van Reuler 1983), and it is likely to be much closer to equilibrium conditions than either Panaitan or the Krakataus. Omitting the peninsula from the analysis lowers the value of z, as may be expected.

Even with Ujung Kulon out of the analysis, the situation is far from a theoretical, textbook one. The Krakataus and Panaitan are certainly not all at equilibrium, if any of them are, and moreover, they are at different stages of species build-up. Panaitan was seriously affected by the 1883 event (Hoogerwerf 1953*b*) but extensive higher areas of the interior were spared. It is likely to be closer to equilibrium than any of the Krakataus. Anak Krakatau is still at an early

TABLE 11. NUMBERS OF SPECIES OF RESIDENT LAND BIRDS FOUND ON THE KRAKATAU ISLANDS, PANAITAN, SEBESI AND UJUNG KULON BY AREA

(Species data for Rakata, Sertung, Panjang and Anak Krakatau are from table 2, assessed records; Panaitan data from Hoogerwerf (1953*a*, *b*) and the Sebesi data from Dammerman (1923) and Chasen (1937). The Ujung Kulon data (Blower & Van der Zon 1977) covers the area west of the isthmus. The area of Anak Krakatau in parenthesis is that covered with vegetation in 1986. Area = surface area of cone same height as island with area of base equal to plan area of island.)

island	number of species	area (km^2)
Rakata (R)	34	12.5
Sertung	26	7.8
Panjang	27	2.7
Anak Krakatau (AK)	24	2.8 (0.14)
Panaitan	66	120.0
Sebesi	31	18.5
Ujung Kulon (UK)	165	300.0

regression: log species versus log area

variables (Sebesi data omitted)	z value (gradient of log versus log plot)
1. AK area = 2.8, R species = 34	0.37
2. AK area = 0.14, R species = 34	0.23
3. AK area = 2.8, R species = 34, UK omitted	0.26
4. AK area = 0.14, R species = 34, UK omitted	0.14

stage of colonization and further from equilibrium than the other Krakatau islands. The flattening of the slope when Ujung Kulon is omitted is probably also due to the inclusion of only one large area near to equilibrium. Rate of increase in species number is not constant, but falls with time, and the difference between observed and equilibrium number for small islands below equilibrium is not proportionately less than for large islands.

As stated above, we include this section not as an example of the species–area relation but rather as an interesting exercise (at the suggestion of an anonymous reviewer).

7. The avifauna of Rakata

Biogeographical analysis of the Krakataus' avifauna may be approached by using only data for Rakata, ignoring Sertung, Panjang and Anak Krakatau. There are several compelling arguments for taking this approach.

(*a*) *Reasons for consideration of Rakata only*

Sertung and Panjang have been inadequately surveyed for birds in the past; Panjang was virtually ignored until the 1980s and Hoogerwerf concentrated on Rakata in 1951. In contrast, Sertung and Panjang were accorded treatment approximately equal to Rakata in our surveys (Thornton & Rosengren 1988; Zann *et al.* 1990*a*). Anak Krakatau, which also received considerable attention in our surveys, did not exist when surveys before 1930 were done, has suffered repeated eruptions, and carried no resident birds in 1951 (Hoogerwerf 1953*a*). Thus our surveys of the archipelago, while providing a baseline for comparison with future work, may be considered inappropriate for comparison with previous surveys, in which the relative coverage of individual islands was different.

Eruptions of Anak Krakatau, which have occurred fairly regularly since its emergence in 1930, are believed to have not only seriously affected its own biota, but also those of Sertung and Panjang (Hoogerwerf 1953*a*; van Borssum Waalkes 1960; Bush *et al.* 1986; Thornton & Rosengren 1988). Rakata evidently has been relatively unaffected, as by far the greater part of its vegetated area, on the southern slopes, was shielded from the volcanic effects by the huge northern cliff scar. Moreover, Anak Krakatau's activity has not only set back the seral succession on Sertung and Panjang, but also may have been responsible for the difference between their forest types and those of Rakata (Bush 1986). Such volcanic episodes will also surely have increased the amount of cryptoturnover on Anak Krakatau, Sertung and Panjang; the chances of populations being successfully founded and extirpated within the intersurvey interval will have increased.

The existence of Anak Krakatau since 1930 also may have perturbed archipelago turnover, as suggested in §6*b*. As a result of its provision of successionally young habitats, immigration to the archipelago may have increased slightly, but because of Anak Krakatau's close proximity to the other islands, extinction from the archipelago would be reduced to a greater extent. That this in fact may have happened is suggested by a comparison of figures 3 and 5. Extinctions on Rakata (the difference between actual and cumulative curves) since canopy closure have been greater than those on the archipelago as a whole. The net result of these effects of the existence and development of Anak Krakatau would be a reduction in turnover on the archipelago.

The above complications are minimized by involving only the course of events on Rakata.

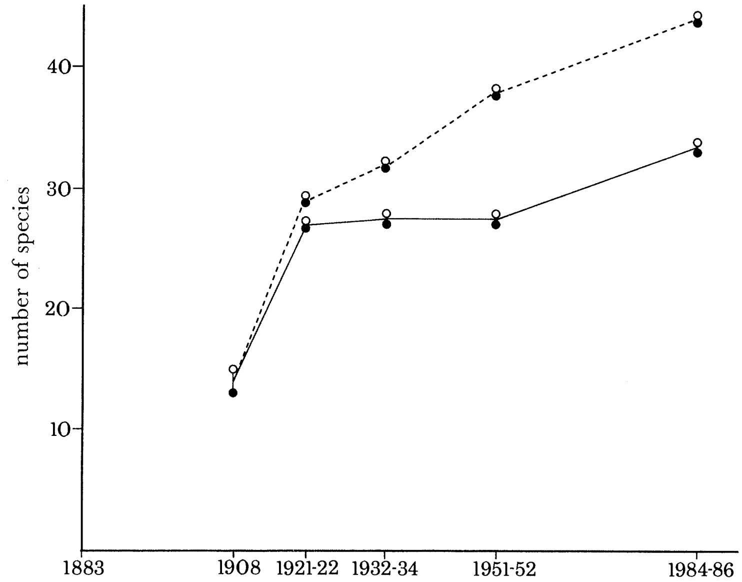

FIGURE 5. Colonization curve of resident land bird species, Rakata. Based on tables 2, 12 and 13. Filled circles, on records; empty circles, on assessment; solid line, actual curve; dashed line, cumulative curve.

Such an approach involves very little loss of data; only one species known from the archipelago has never been recorded from Rakata: *Centropus sinenis*.

(*b*) *The species–time curve for Rakata and the time of 'bird zero'*

Calculating the equilibrium number for Rakata from the last two data points in the way outlined in §6*c*, $\hat{S}$ is 51 on unadjusted records and 56 on assessed data; if the large-billed crow is discounted, the estimates are reduced to 48 and 52, respectively. If cryptoturnover was the same as found for the archipelago (§5*c*), the estimate of $\hat{S}$ would be reduced (by using equation 14) by 37%, to 33–35 species. The constant number of species on the island for the second, third and fourth surveys (tables 12, 13) contrasts with the gradual rise in numbers on the archipelago during those three decades (tables 5 and 6). Equation 15 (§6*c*) cannot be fitted to all the Rakata data within the range limits imposed for surveys that included ornithologists, suggesting (with the shape of the curve itself) a more complex situation such as the achievement of a 'pseudoequilibrium' followed by a further increase in species number. The existence of the Sertung spit and eruptions on Anak Krakatau, which affected Rakata very much less than the other islands, provided a more heterogeneous environment for the archipelago as a whole than was present on Rakata. The rather marked increase in Rakata's species number since 1951 is largely a result of the addition of aerial predators and insect feeders such as the oriental hobby, black eagle, barn owl, house swift, Pacific swallow and brahminy kite, some of which may be expected to be wide-ranging and feeding over the archipelago generally, and since 1951, open country on Anak Krakatau was available in addition to the small area on the Sertung spit.

It is extremely unlikely that permanent establishment by land birds began in 1883, thus to require 'bird zero' to be the eruption date of the island of Krakatau, 1883, is quite unrealistic.

Although the whole of the Rakata data cannot be fitted by a simple exponential curve it is possible to fit equation 15 to the first three data points, with the following values: $t_r = 4.8$ years, $\hat{S} = 28.1$ species, $t_0 = 21.0$ years. This implies that bird zero was 1904 $(1883 + t_0)$. The $\hat{S}$ value,

Table 12. Turnover of resident land bird species on Rakata, based on survey records

intersurvey period	I		II		III		IV		V	
survey date		1908		1919–21		1932–34		1951–52		1984–85
intersurvey interval (years)	25		12		13		18.5		33	
actual number of species		13		27		27		27		33
cumulative number of species		13		29		32		38		44
gains		13		16		3		6		12
losses		—		2		3		6		6
I (immigration rate)	0.52		1.33		0.23		0.32		0.36	
E (extinction rate)	—		0.17		0.23		0.32		0.18	
C (colonization rate)	0.52		1.17		0.00		0.00		0.18	
T (turnover rate)	0.26		0.75		0.23		0.32		0.27	
λ_s (acquisition rate coefficient) × 100	8.00		6.67		0.85		1.20		1.21	
μ_s (extinction rate coefficient) × 100	—		0.83		0.85		1.20		0.61	
γ (colonization rate coefficient) × 100	8.00		5.83		0.00		0.00		0.61	
τ (turnover rate coefficient) × 100	4.00		3.75		0.85		1.20		0.91	
λ_{sp} (pool immigration rate coefficient*) × 100	0.33		0.92		0.17		0.24		0.27	

* With assumed pool of 165 species.

Table 13. Turnover of resident land bird species on Rakata, based on assessment of survey records

intersurvey period	I		II		III		IV		V	
survey date		1908		1919–21		1932–34		1951–52		1984–85
intersurvey interval (years)	25		12		13		18.5		33	
actual number of species		15		27		28		28		34
cumulative number of species		15		29		32		38		44
gains		15		14		3		6		11
losses		—		2		2		6		5
I (immigration rate)	0.60		1.17		0.23		0.32		0.33	
E (extinction rate)	—		0.17		0.15		0.32		0.15	
C (colonization rate)	0.60		1.00		0.08		0.00		0.18	
T (turnover rate)	0.30		0.67		0.19		0.32		0.24	
λ_s (acquisition rate coefficient) × 100	8.00		5.56		0.84		1.16		1.08	
μ_s (extinction rate coefficient) × 100	—		0.79		0.56		1.16		0.49	
γ (colonization rate coefficient) × 100	8.00		4.76		0.28		0.00		0.59	
τ (percentage turnover rate) × 100	4.00		3.17		0.70		1.16		0.78	
λ_{sp} (pool immigration rate coefficient*) × 100	0.38		0.81		0.17		0.24		0.25	

* With assumed pool of 165 species.

however, is clearly an underestimate; there are already 34 species on Rakata. Fitting the equation to the first two data points and our own survey data, $t_r = 12.6$ years, $\hat{S} = 34.5$ species and $t_0 = 17.5$ years, implying that bird zero was in 1901. A more reliable estimate of t_0, from all the data for the whole archipelago (§6*c*) was found to be 10.3 years, and bird zero thus at the beginning of 1894.

These estimates suggest that birds first successfully colonized Rakata only in the second decade after 1883.

In 1897 (14 years post-eruption) 37 seed-plant species and 13 pteridophytes were present on the island. A dense grassland had replaced the fern cover except at higher elevations, the '*pescaprae* formation' was established on the beaches and a coastal '*Barringtonia* woodland association' was developing (Penzig 1902). Nine years later (1906) the number of vascular plants had doubled, to 99, and 88 of these were seed plants, 11 peteridophytes. The *Barringtonia* association had developed into a scattered coastal woodland. It was not until two years later (1908) that patches of woodland incorporating secondary forest species were found (Backer 1909). Thus 1894–1903 evidently was a time when the number of spermatophyte species was increasing very rapidly, and just before the beginning of the secondary forest development.

At the time of the first zoological survey (1908) there were no granivorous birds on the island, yet between 1896 and 1905 there were two sedges and seven grass species. It is unlikely that birds exploited the extensive grassland phase and yet did not survive until 1908; we suggest that this phase was 'missed' by granivorous birds. Only one obligate granivore colonized since that time (*Geopelia striata*) and did not persist, and grassfinches have never been recorded on the island.

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