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ISLAND BIOGEOGRAPHY AND THE CONSERVATION OF NEW ZEALAND'S INDIGENOUS FOREST-DWELLING AVIFAUNA[3]

Summary: It will be necessary to establish reserves for the conservation of New Zealand's forest avifauna largely in the absence of detailed autecological studies. Hence the empirical findings of island biogeography may provide the best available guide to the reserve size necessary for the preservation of both species communities and individual species. The occurrence of indigenous forest birds on offshore islands suggests that reserves of the order tens of km^2 or larger of comparable forest habitat may be necessary on the mainland to ensure a high probability of the long-term survival of all species which still occur there. The area requirements of individual species tend to increase with the degree of endemism and reliance on indigenous forest habitats.

Keywords: Island biogeography; island avifauna; forest avifauna; forest patches; reserves; conservation; New Zealand.

Introduction

The application of island biogeography to conservation, in particular the use of the equilibrium model (MacArthur and Wilson, 1967) to justify the conservation of single large reserves rather than several small ones of equivalent total area (Terborgh, 1974; Diamond, 1975a, 1976) has been criticized increasingly in recent years (e.g., Simberloff and Abele, 1976, 1982; Gilbert, 1980; Higgs and Usher, 1980; Higgs, 1981; McCoy, 1982, 1983; Margules, Higgs and Rafe, 1982). These criticisms have revealed that there is no general answer to the question whether a single large reserve will conserve more species than several small ones of the same total area. Nevertheless, this does not alter the empirical fact that the number of species of many taxa on islands is strongly area-dependent, which has major relevance to the conservation of species communities (e.g., Wilcox, 1980). In addition, observations on the effects of island size on species occurrence may provide a useful guide to the minimal area required by self-sustaining remnants of individual species, through the use of incidence functions (Diamond. 1975b, 1978).

The problem of whether a single large reserve is preferable to several small ones of equivalent total area arises much less frequently in conservation practice than the question how large should each individual reserve be, i.e., are large reserves necessary or will a similar number of small reserves (of much smaller total area) suffice? The problem is often which of a series of fragments of natural habitat have the greatest conservation value. In this situation detailed information on species' distributions may provide a more accurate guide than species-area relationships to the reserve size necessary for effective conservation of natural communities (McCoy, 1983). However, distributional data must be interpreted with care if they are not obtained over a sufficiently long period to measure the extent of species turnover or the rate of local extinctions following isolation. Species distributions may give a mis-leading picture in recently isolated fragments of natural habitat (e.g., Soule, Wilcox and Holtby, 1979; East, 1981, 1983).

Several critics of the application of island biogeography to conservation have emphasized that autecological studies of the target species will provide a much sounder basis for their conservation (e.g., Higgs, 1981). Gilpin and Diamond (1980) pointed out that conservation must also be based on an evaluation of each species' value, since species with different area requirements will be favoured by different conservation strategies. In practice, irreversible conservation decisions frequently have to be made in the absence of detailed ecological knowledge, as in the case of New Zealand's indigenous forest birds.

Unmodified lowland (< 300 m asl) indigenous forest appears to be vital for the continued existence of abundant, diverse communities of indigenous forest birds (Dawson *et al.,* 1978; Onley, 1980, 1983; Dawson, 1984). Current proposals to log, clearfell or convert to exotic plantations substantial areas of the remaining indigenous lowland forest underline the need to create adequate reserves for the conservation of forest birds on the mainland in the near future (e.g., Saunders, 1983; Dawson, 1984). These reserves will have to be established with only a preliminary knowledge of the habitat

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requirements of most species (e.g., Dawson *et al.*, 1978). In this situation, the empirical findings of island biogeography may provide a useful, if approximate guide to the minimal reserve sizes necessary for self-sustaining forest bird communities. Hackwell (1982) showed that the size of mainland forest isolates has a major influence on the size and composition of forest bird communities. This paper uses information gathered by Williams (1981) to assess the effects of the size of offshore islands on the occurrence of indigenous forest birds.

Sources of Data

The occurrence of indigenous forest-dwelling birds i.e. native birds which breed in indigenous forest, was taken from the species lists given for offshore (land-bridge) islands by Williams (1981, appendix 2). These lists represent the maximum number of species regarded as having been resident breeders up to and including the period of European settlement (see Williams (1981) for the criteria used in drawing up the species lists). Stephens and White Islands were excluded for the reasons discussed by Williams (1981). Data were also included from several islands (mainly < 1 km^2) which Williams (1981) did not consider: Rurima, Motuhoropapa, Allport, Open Bay, Mokohinau, Motuara, Maud and Rakitu (Arid) Islands (sources: Bell and Brathwaite

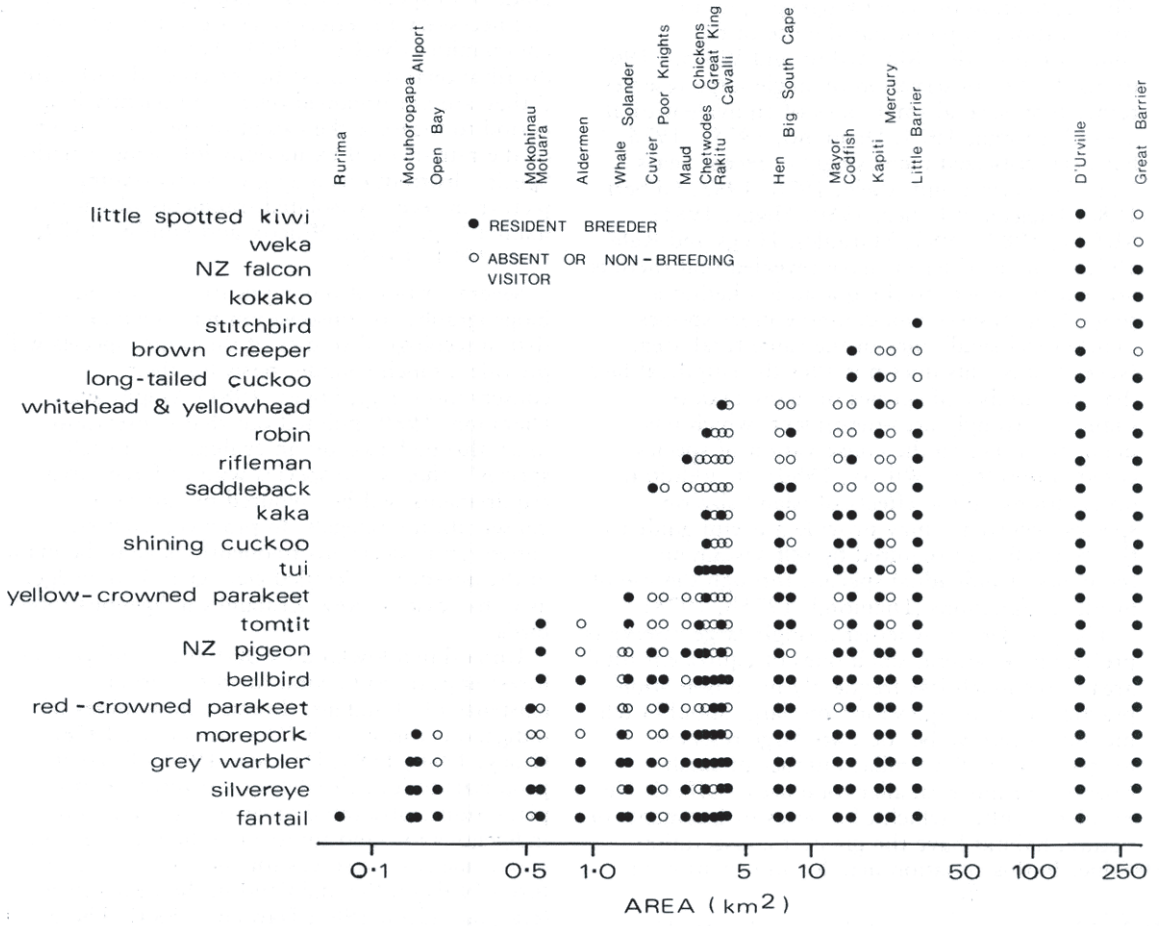

Figure 1: *Occurrence of indigenous forest-dwelling birds on offshore islands of different size. For each species, symbols indicating absence are shown only for those islands larger than the smallest occupied as a resident breeder.*

(1964), Stirling and Johns (1969), Imboden (1978), files of the New Zealand Wildlife Service, Department of Internal Affairs, and the authors' personal observations). Most of these islands are 1-50 km from the mainland (which comprises North, South and Stewart Islands). A few, e.g., D'Urville (which Williams (1981) treated as part of the mainland) and Maud Islands, are less than 1 km from the mainland.

Occurrence of Indigenous Forest Birds on Offshore Islands

The 26 offshore islands included in this study range in size from 0.07 to 300 km^2. Figure 1 illustrates the change in the species composition of indigenous forest bird communities with island area. The species-area relationship for indigenous forest birds on offshore islands is shown in Figure 2.

These islands and the mainland formed a single land mass at the time of the last maximum glaciation about 15,000 years ago, but have comprised an archipelago for at least the last 10,000 years (Stevens, 1980). They were largely covered with various forms of lowland forest at the time of European settlement. Some islands, e.g. Great Barrier and D'Urville, have been extensively modified in the last 100 years by forest clearance, agricultural development and introduced mammals, with a consequent loss of some indigenous forest bird species. The avifaunas of the remaining unmodified offshore islands appear to be stable with very low species turnover rates (Williams, 1981). Figure 1 therefore indicates the effects of island area on the long-term survival of forest bird species in unmodified lowland forest habitats.

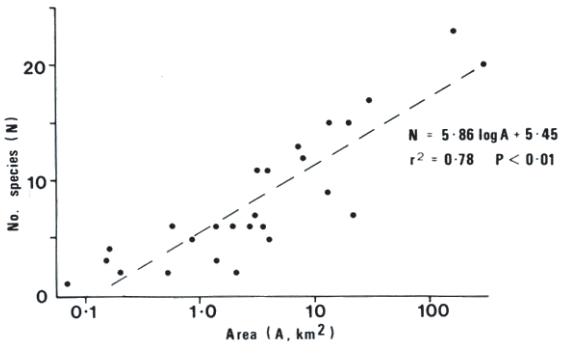

Figure 2: *Relationship between number of resident forest-dwelling bird species and island area. Data from Figure* 1 *with the addition of two extinct species, bush wren on Big South Cape Island and piopio on D'Urville Island (Williams,* 1981; *appendix* 2). *The linear-log model provides a slightly better fit than the conventional log.-log. model.*

There are insufficient islands in our sample to plot incidence functions (Diamond, 1975b) accurately, but Figure 1 shows that as island area declines species loss tends to occur sequentially in a predictable manner. The two largest offshore islands, Great Barrier (300 km^2) and D'Urville (162 km^2), had an almost full complement of the species listed in Figure 1. Most species of forest birds are widespread on the mainland. The few species absences from the two largest islands (Fig. 1) are mostly cases where the adjacent mainland lies outside the species' recent geographical range, e.g., little spotted kiwi *(Apteryx owenii)* and brown creeper *(Finschia novaeseelandiae)* from Great Barrier (Little Barrier, Mercury and Kapiti Islands also lie outside the brown creeper's range), and stitch bird *(Notiomystis cincta)* from D'Urville.

Apart from the falcon *(Falco novaeseelandiae),* the species with the largest area requirements, i.e., those restricted to one or both of the two largest islands (Fig. 1), are characterised by partial or complete loss of flight and a high level of endemism, viz., order or suborder (little spotted kiwi), family (kokako *Callaeas cinerea),* and genus (weka *Gallirallus australis).* The extinct piopio *(Turnagra capensis),* the only known member of the endemic family Turnagridae, also occurred on D'Urville. Most of these species are (or were) highly dependent on indigenous forest habitats, but the weka may be primarily a forest edge species (Coleman, Warburton and Green, 1983). The falcon occurs in a variety of habitats besides indigenous forest and is now largely confined to upland areas on the mainland. The minimal area requirements of these species on offshore islands lie somewhere between 30 and 162 km^2; there are no offshore islands in this size range.

Additional species which are absent from most or all islands smaller than 15 km^2 (Codfish) to 30 km^2 (Little Barrier) are mainly dependent on indigenous forest. All of these birds belong to endemic families (rifleman *Acanthisitta chloris* and saddleback *Philesturnus carunculatus),* genera (brown creeper, whitehead *Mohoua albicilla* and yellowhead M. *ochrocephala)* or species (stitchbird, long-tailed cuckoo *Eudynamys taitensis* and robin *Petroica australis).*

Other birds in Figure 1 which are largely dependent on indigenous forest occur less frequently as island size declines below 10 km^2 and are absent from most or all islands smaller than 1 km^2. This group includes kaka *(Nestor meridionalis),* tui *(Prosthemadera novaeseelandiae),* yellow-crowned parakeet *(Cyanoramphus auriceps),* red-crowned parakeet *(C. novaezelandiae),* and pigeon *(Hemiphaga novaeseelandiae),* all of which belong to endemic genera, and tomtit *(Petroica macrocephala)* which is an endemic species. The shining cuckoo *(Chrysococcyx lucidus),* a non-endemic species which is not dependent on indigenous forest, shows a similar pattern of occurrence to kaka. The bellbird *(Anthornis melanura),* which belongs to an endemic genus, occurs in indigenous forest, scrublands and exotic forests especially those close to indigenous forest (Clout, 1980) and is found on most islands larger than about 0.5 km^2 (Fig. 1).

The four smallest islands in Figure 1 range in size from 0.07 km^2(Rurima) to 0.20 km^2 (Open Bay). None of the species which occur as resident breeders on these islands, morepork *(Ninox novaeseelandiae),* grey warbler *(Gerygone igata),* silvereye *(Zosterops lateralis)* and fantail *(Rhipidura fuliginosa),* are dependent on indigenous forest. These species also occur widely in exotic forests and in other highly modified rural and urban habitats. This group of birds with low area requirements includes only one endemic species, the grey warbler.

There is thus a disproportional loss of species showing a high level of endemism and dependence on indigenous forest as island area declines from > 100 km^2 to < 1 km^2. Similar predictable, sequential patterns of natural species loss with declining area have been observed elsewhere on both islands (e.g., Diamond, 1972) and mainland forest isolates (e.g., Moore and Hooper, 1975; Galli, Leck and Forman, 1976; Whitcomb *et al.,* 1981).

Implications for Conservation on the Mainland

Conservation of species communities

New Zealand's indigenous forest avifauna at the time of European settlement comprised about 30 species. Three of these, bush wren *(Xenicus longipes),* huia *(Heteralocha acutirostris)* and pio pio are now believed to be extinct (Williams and Given, 1981). The 27 surviving species include three flightless species which occur naturally only on the mainland, brown kiwi *(Apteryx australis),* great spotted kiwi *(A. haastii)* and kakapo *(Strigops habroptilus),* plus the species listed in Figure 1. We have excluded orange-fronted parakeet *(Cyanoramphus malherbi)* because of its uncertain taxonomic status (Nixon, 1981).

The little spotted kiwi, stitch bird and saddleback now survive only on offshore islands where they occur naturally or have been introduced. The mainland population of kakapo has been reduced to small remnants on Stewart Island and in Fiordland (Williams and Given, 1981). The red-crowned parakeet is also now very rare on the mainland, but is still abundant on some offshore islands. Six of the remaining 22 species, brown and great spotted kiwis, weka, kokako, whitehead and yellowhead now occur locally on the mainland. The other 16 species of indigenous forest birds are still widespread on the mainland, although the distributions of some have contracted markedly in the last 100 years, e.g. falcon, kaka, yellow-crowned parakeet and robin. Most of these widespread species plus a few of the six localised species still occur in the remaining extensive areas of mainland indigenous forest which include substantial remnants of lowland forest, giving a typical indigenous forest bird community of about 15 to 20 species (e.g., Dawson *et at.,* 1978).

The species-area relationship for forest birds on offshore islands (Fig. 2) suggests that reserves of at least tens of km^2 are necessary for the long-term survival of diverse forest bird communities (15 to 20 indigenous species) in comparable habitat on the mainland. Species-area curves do not provide a precise guide to the reserve size necessary to conserve a particular number of species because of the effects of variables other than area, such as habitat quality (e.g., McCoy, 1983). Nevertheless, species-area relationships do indicate the order of magnitude of the area necessary for effective conservation of natural communities. The smallest offshore island which supports at least 15 species of indigenous forest birds is Codfish (15 km^2).

Conservation of individual species

The aim of conservation is usually to preserve certain species or groups of species rather than entire species communities. Endemic birds reliant on indigenous forest which are the species most likely to be lost as offshore island size declines

below 10 km^2 include a high proportion of the species in greatest need of conservation. Little spotted kiwi, kokako, stitch bird and saddleback were listed as rare, vulnerable or endangered by Williams and Given (1981), and yellowhead, robin and kaka are approaching this status (Crawley, 1982). These species generally have large or very large area requirements for long-term survival on offshore islands (Fig. 1). Other species which can be given high conservation priority because they are ancient endemics include rifleman, which also appears to have a large area requirement (Fig. 1) and four flightless species, brown and great spotted kiwis, weka and kakapo.

Many offshore islands contain favourable habitat for flightless indigenous birds. This is illustrated by the successful introductions of brown kiwi to Little Barrier and Kapiti Islands and little spotted kiwi to Kapiti in the early 1900s. The weka has been introduced successfully to islands as small as the Open Bay Islands. The natural absence of these flightless species from most or all offshore islands may reflect large area requirements, at least for some species.

There are three possible explanations for the complete absence of the brown kiwi from offshore islands. This species may never have occupied any islands (this seems unlikely since all of New Zealand's offshore islands were connected to the mainland during the last glaciation, although subfossil remains of kiwis have not. been found on them), it may have been exterminated on islands by Maoris or earlier Polynesians (possible), or it may have died out naturally over the last 10,000 years because after their isolation none of the islands was large enough to support self-sustaining populations in the long term. Flightless species such as kiwis would be unlikely to recolonise offshore islands from the mainland. Genetic considerations suggest that a population of at least 500 to 1,000 individuals is necessary to ensure a high probability of long-term survival under natural conditions (Frankel and Soule, 1981). Brown kiwi population density is approximately 30 per km^2 in Northland state forests such as Waitangi with its mixture of exotic and indigenous vegetation, and Waipoua, which. is solely indigenous forest (Colbourne and Kleinpaste, 1983; R. Kleinpaste, pers. comm.). This suggests that the area necessary for a population of 500-1000 birds could be 17-33 km^2. Large offshore islands such as Kapiti (20 km^2) and Little Barrier (30 km^2) may be of a similar order to, or less than, the minimum area necessary for the long-term survival (i.e. over thousands of years) of brown kiwi under natural conditions. A similar argument could apply to the largest offshore islands, D'Urville (162 km^2) and Great Barrier (300 km^2), since 500-1000 individuals may be an underestimate of the minimum population for long-term survival (Frankel and Soule, 1981) and only parts of these islands would provide suitable habitat for kiwis.

Similar factors may account for the absence of other poor or non-fliers from the larger offshore islands. For example, recent estimates of kokako population density (J. R. Hay, pers. comm.) suggest that the total area of islands such as Little Barrier and Kapiti may be similar to or below the minimal area necessary to support a population of 500 to 1,000 birds. The wide fluctuations of weka populations, with local extinctions and subsequent recolonisations, which are known to occur on the mainland (Coleman *et al*., 1983) may give this species a propensity to die out on islands in the long term. This may account for its natural absence from all offshore islands except D'Urville Island (Fig. 1), which may be close enough to the mainland (500 m) for the weka to have recolonized it by swimming (d. Wright, 1981).

There is clearly a general tendency for the species in greatest need of conservation to have large area requirements. This underlines the value of the larger, relatively unmodified offshore islands which are partially or completely free of introduced mammals, such as Little Barrier and Kapiti, for the long-term conservation of indigenous forest birds. These islands are valuable repositories for species which appear unable to survive in the presence of introduced mammals on the mainland, viz., little spotted kiwi, stitchbird, saddleback, and possibly others such as kakapo. However, preservation on offshore islands is not an adequate substitute for the conservation of . species within their natural habitats on the mainland where this is possible (Crawley, 1982).

Figure 1 suggests that large reserves (tens or hundreds of km^2) of comparable forest habitat to that on unmodified offshore islands may be necessary to ensure a high probability of the long-term survival of species such as kiwis, weka, kokako, brown creeper, long-tailed cuckoo, whitehead, yellowhead, robin, rifleman, kaka and yellow-crowned parakeet on the mainland. Other species of indigenous forest birds have smaller area requirements (Fig. 1) and are generally

widespread on the mainland. Reserves which are sufficiently large to support self-sustaining populations of the more vulnerable species should therefore also be adequate for entire species communities. In contrast, isolated small reserves <1 km^2) of comparable habitat to offshore islands may support only a few species (Fig. 1), most of which occur widely in other habitats besides indigenous forests. The need for large reserves to preserve vertebrate species which are highly dependent on unmodified natural habitats is becoming increasingly apparent (e.g., Whitcomb *et al.,* 1981; Humphreys and Kitchener, 1982).

How comparable are mainland and offshore island habitats?

Use of the incidence of occurrence on islands to assess the effects of area on the probability of a species' long-term survival assumes that all of the islands included in the analysis comprise similar habitats. In practice, species' absences from some islands may reflect lack of suitable habitat rather than island size. For this reason, incidence functions may often give only an approximate guide to a species' area requirements. In addition, Figure 1 shows the occurrence of forest birds on offshore islands in their unmodified state, whereas all of New Zealand's mainland forests are now modified to some extent by introduced mammals.

Both predatory and browsing mammals have reduced the quality of mainland indigenous forests as habitats for indigenous birds (e.g., Leathwick, Hay and Fitzgerald, 1983) and may have allowed the ingression of exotic species (Diamond and Veitch, 1981). Consequent reductions in the population densities of indigenous forest birds on the mainland may result in larger area requirements for self-sustaining populations than indicated in Figure 1. Conversely, the vegetation on small offshore islands does not attain the structural or species diversity characteristic of inland virgin lowland forests on the mainland, because of the predominance. of coastal effects such as wind-blown salt spray. This impoverished vegetation might result in small offshore islands supporting fewer species of indigenous forest birds than similar-sized, isolated remnants of lowland forest on the mainland.

In practice, the occurrence of indigenous birds in mainland forest isolates (Hackwell, 1982) indicates similar effects of area on species occurrence to those observed on offshore islands (Fig. 1). Hackwell's analysis referred mainly to Northland but similar patterns of occurrence in mainland forest isolates are apparent elsewhere. On the Mamaku Plateau, for example, brown kiwi, kaka and kokako are now mainly restricted to the largest remnant patches (tens to hundreds of km^2) of indigenous forest (Saunders, 1983). These similarities indicate that Figure 1 may provide a realistic guide to the areas of indigenous forest necessary for the long-term survival of forest birds on the mainland. Dawson (1984) concluded that the size of some mainland forest reserves should be of the order hundreds of km2, to preserve bird species with very large area requirements.

The importance of species' dispersal abilities

Most species of indigenous forest birds occur as resident breeders on at least one relatively small (< 5 km^2) offshore island (Fig. 1). This suggests that it might be possible to preserve at least some species with large area requirements on relatively small islands or mainland reserves which comprise 'hot spots' (Diamond, 1975b) of especially favourable habitat. For example, Cuvier Island (1.9 km^2) is the smallest island on which the saddleback occurred naturally. Following its extermination there by feral cats the saddleback was successfully reintroduced after the cats were eliminated. It has increased since to a stable population of about 800 individuals on Cuvier, which provides a nucleus of birds for reintroduction to other suitable islands (Lovegrove and O'Callaghan, 1982).

In some cases the smallest island occupied may be too small to support a self-sustaining population in the absence of immigration from nearby larger islands or the mainland. Some forest bird species are capable of considerable interisland movements. Imboden (1978) recorded tuis banded on Tiritiri Island visiting Motuhoropapa Island, 15 km away across open sea (these birds could have travelled by a more circuitous route via the mainland, involving smaller water gaps). Bell and Brathwaite (1964) recorded a kaka flying at least 3 km from Great Barrier Island to Rakitu Island, where the kaka population at the time of their survey was estimated to comprise only five individuals. The whitehead appears to have died out on Rakitu in the last 20 years (Bellingham *et al.,* 1982) following its earlier extinction on Great Barrier. This may reflect the decline in the indigenous forest cover of Rakitu as well as the loss of a nearby source of birds on Great Barrier.

While significant species number-distance relationships are not apparent for New Zealand's outlying islands, it is possible that individual islands within compact offshore island groups may support a greater number of species than if they were more isolated (Williams, 1981). Such island groups have been treated as single islands in our analyses. For example, the smallest offshore island on which the robin occurs naturally is Outer Chetwode (0.8 km^2). It is not known whether it would have survived there in the absence of the adjacent population on Inner Chetwode Island (2.4 km^2). We have used the combined area of these two islands (3.2 km^2) in Figures 1 and 2.

Similar closely-spaced archipelagos of forest patches may occur on the mainland, as on Banks Peninsula. Here remnants of the original mixed podocarp/broadleaf forest survive in 26 scenic reserves (total area 7.9 km^2) and on adjacent private land lying within a radius of about 20 km. The persistence of species such as rifleman and brown creeper, which have large area requirements on offshore islands (Fig. 1), in isolates as small as the Okuti Valley Scenic Reserve (0.04 km^2) on Banks Peninsula (McCaskill, 1974) may depend on movement of individuals making this and other small forest remnants effectively a single, larger habitat island.

The dispersal biology of the target species is an essential consideration in conservation planning (Diamond, 1978), but little is known about the minimum distance between separate patches of forest at which they become isolated as habitats for forest birds. This will depend on the ability (and willingness) of birds to move between them. A series of groups of small, closely-spaced forest isolates, each group comprising a large enough area in total to support self-sustaining populations, may be adequate for the long-term conservation of many species of New Zealand's indigenous forest birds. Such a system of small reserves may be sufficient for at least the more mobile species, although it may subject forest-dependent species to strong competition from species such as silvereye which invades indigenous forest remnants in large numbers from surrounding modified habitats in autumn and winter (Fitzgerald and Fitzgerald, 1983). Very large individual reserves (at least tens of km^2) might also be unnecessary for species with limited mobility and large area requirements if enough was known about their ecology to manage small populations effectively. Intensive management demands detailed research to provide the necessary background information. In practice, such research on endangered species tends to coincide with rather than precede the implementation of management procedures (Crawley, 1982). The effective management of forest bird populations will require detailed knowledge of such factors as the ability of different species to utilise various types of indigenous forest (e.g., upland, lowland, unmodified, modified and finer subdivisions of these categories, and successional stages), as well as dispersal ability.

Some forest birds have already been reduced to the level where their long-term survival probably depends on intensive management, such as habitat manipulation and the translocation of individuals to prevent genetic isolation of small subpopulations on offshore islands or the mainland. The little spotted kiwi and kakapo are now reduced to total populations of no more than a few hundred birds (Williams and Given, 1981) and kokako to perhaps 1,000 individuals (Saunders, 1983). A conservation strategy which excludes large mainland reserves of suitable habitat may have an unacceptably high risk of eventually reducing to a similar status other indigenous forest birds which appear to have large or very large area requirements, such as brown kiwi, whitehead, yellowhead, robin, rifleman and kaka. Species for which upland indigenous forests (> 750 m asl) provide a suitable year-round habitat, e.g., rifleman, are adequately catered for in New Zealand's present system of mainland forest reserves. This may not be the case for the majority of indigenous forest bird species, which appear to prefer unmodified lowland forest (Dawson, 1984).

Conclusion

The empirical findings of island biogeography may provide a useful guide to at least the order of magnitude of the reserve sizes necessary for the conservation of New Zealand's indigenous forest avifauna, in the absence of detailed information on the target species' ecological requirements. The occurrence of indigenous forest birds on unmodified offshore islands suggests that it would be prudent to set aside some reserves of at least tens of km^2, and preferably hundreds of km^2, of suitable habitat on the mainland, to ensure a high probability of the long-term survival of all species which still occur there.

These findings highlight the importance of two recent government decisions. These were to add 170 km^2 of unlogged lowland rimu *(Dacrydium cupressinum)*-dominant forest and wetlands, including important brown kiwi habitat, to the existing, largely mountainous Westland National Park (918 km^2), and to protect permanently from logging a large part (60 km^2) of the West Taupo forests, which contain the largest surviving population of kokako.

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